Zoological articles contributed to the "Encyclopaedia Britannica" / by E. Ray Lankester, to which are added kindred articles by W. Johnson Sollas ... [et al.].

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Classes of the Mollusca.—The classes of the Mollusca which we recognize are as follows :—

Phylum MOLLUSCA.

BRANCH A.—**Glossophora.**

Class 1.—GASTROPODA.
  Br. a.—Isopleura.
    Examples — Chiton, Neomenia.
  Br. b.—Anisopleura.
    Examples—Limpet, Whelk, Snail, Slug.
Class 2.—SCAPHOPODA.
    Example—Tooth-shell.
Class 3.—CEPHALOPODA.
  Br. a.—Pteropoda.
    Examples—Hyalæa, Pneumodermon.
  Br. b.—Siphonopoda.
    Examples — Nautilus, Cuttles, Poulp.

BRANCH B.—**Lipocephala** (=Acephala, *Cuvier*).

Class 1.—LAMELLIBRANCHIA (Syn. Conchifera).
    Examples—Oyster, Mussel, Clam, Cockle.

General Characters of the Mollusca.—The forms comprised in the above groups, whilst exhibiting an extreme range of variety in shape, as may be seen on comparing an Oyster, a Cuttle-fish, and a Sea-slug such as Doris; whilst adapted, some to life on dry land, others to the depths of the sea, others to rushing streams ; whilst capable, some of swimming, others of burrowing, crawling, or jumping, some, on the other hand, fixed and immobile; some amongst the most formidable of carnivores, others feeding on vegetable mud, or on the minutest of microscopic organisms—yet all agree in possessing in common a very considerable number of structural details which are not possessed in common by any other animals.

The structural features which the Mollusca do possess in common with other animals belonging to other great phyla of the animal kingdom are those characteristic of the Cœlomata, one of the two great grades (the other and lower being that of the Cœlentera) into which the higher animals, or Enterozoa as distinguished from the Protozoa, are divided (**13**). The Enterozoa all commence their individual existence as a single cell or plastid, which multiplies itself by transverse division. Unlike the cells of the Protozoa, these embryonic cells of the Enterozoa do not remain each like its neighbour and capable of independent life, but proceed to arrange themselves in two layers, taking the form of a sac. The cavity of the two-cell-layered sac or Diblastula thus formed is the primitive gut or ARCH-ENTERON. In the Cœlentera, whatever subsequent changes of shape the little sac may undergo as it grows up to be Polyp or Jelly-fish, the original arch-enteron remains as the one cavity pervading all regions of the body. In the Cœlomata the arch-enteron becomes in the course of development divided into two totally distinct cavities shut off from one another—an axial cavity, the MET-ENTERON, which retains the function of a digestive gut; and a peri-axial cavity, the CŒLOM or body-cavity, which is essentially the blood-space, and receives the nutritive products of digestion and the waste products of tissue-change by osmosis. The Mollusca agree in being Cœlomate with the phyla Vertebrata, Platyhelmia (Flat-worms), Echinoderma, Appendiculata (Insects, Ringed-worms, &c.), and others,—in fact, with all the Enterozoa except the Sponges, Corals, Polyps, and Medusæ.

In common with all other Cœlomata, the Mollusca are at one period of life possessed of a PROSTOMIUM or region in front of the mouth, which is the essential portion of the "head," and is connected with the property of forward locomotion in a definite direction and the steady carriage of the body (as opposed to rotation of the body on its long axis). As a result, the Cœlomata, and with them the Mollusca, present (in the first instance) the general condition of body known as BILATERAL SYMMETRY; the dorsal is differentiated from the ventral surface, whilst a right and a left side similar to, or rather the complements of, one another are permanently established. In common with all other Cœlomata, the Mollusca have the mouth and first part of the alimentary canal which leads into the met-enteron formed by a special invagination of the outer layer of the primitive body-wall, not to be confounded with that which often, but not always, accompanies the antecedent formation of the arch-enteron; this invagination is termed the STOMODÆUM. Similarly, an anal aperture is formed in connexion with a special invagination which meets the hinder part of the met-enteron, and is termed the PROCTODÆUM.

In common with many (if not all) Cœlomata, the Mollusca are provided with at least one pair of tube-like organs, which open each by one end into the cœlom or body cavity, and by the other end to the exterior, usually in the neighbourhood of the anus. These are the NEPHRIDIA.

Like all other Cœlomata, the Mollusca are also provided with special groups of cells forming usually paired or median growths upon the walls of the cœlomic cavity, the cells being specially possessed of reproductive power, and differentiated as egg-cells and sperm-cells. These are the GONADS. As in other Cœlomata, the cells of the gonads may escape to the exterior in one of two ways—either through the nephridia, or, on the other hand, by special apertures.

As in all other Cœlomata, the cells, which build up respectively the primary outer layer of the body, the lining layer of the met-enteron, and the lining layer of the cœlom, are multiplied and differentiated in a variety of ways in the course of growth from the early embryonic condition. TISSUES are formed by the adhesion of a number of similarly modified cells in definite tracts. As in all Cœlomata, there is a considerable variety of tissues characterized by, and differentiated in relation to, particular physiological activities of the organism. Not only the Cœlomata but also many Cœlentera show, in addition to the EPITHELIA (the name given to tissue which bounds a free surface, whether it be that of the outer body-wall, of the gut, or of a blood-space), also deeper lying tissues, of which the first to appear is MUSCULAR tissue, and the second NERVOUS tissue.

The epithelia are active in throwing off their constituent cells (blood-corpuscles from the wall of the cœlom), or in producing secretions (glands of body-wall and of gut), or in forming horny or calcareous plates, spines, and processes, known as CUTICULAR PRODUCTS (shells and bristles of the body-wall, teeth of the tongue, gizzard, &c.).

In the Mollusca, as in all other Cœlomata, in correspondence with the primary bilateral symmetry and in relation to the special mechanical conditions of the prostomium, the nervous tissue which is in Cœlentera, and even in Flat-worms, diffused over the whole body in networks, tends to concentrate in paired lateral tracts, having a special enlargement in the prostomium. The earlier plexiform arrangement is retained in the nervous tissue of the walls of the alimentary canal of many Cœlomata, whilst a concentration to form large nerve-masses (GANGLIA), to which numerous afferent and efferent fibres are attached, affects the nervous tissue of the body-wall.

In all Cœlomata, including Mollusca, muscular tissue is developed in two chief layers, one subjacent to the deric or outer epithelium (SOMATIC MUSCULATURE), and a second surrounding the alimentary canal (SPLANCHNIC MUSCULATURE). Thus, primarily, in Cœlomata the body has the character of two muscular sacs or tubes, placed one within the other and separated from one another by the cœlomic space. The somatic musculature is the more copious and develops very generally an outer circular layer (*i.e.*, a layer in which the muscular fibres run in a direction transverse to the long axis of the body) and a deeper longitudinal layer; to these oblique and radiating fibres may be added. The splanchnic musculature, though more delicate, exhibits a circular layer nearer the enteric epithelium, and a longitudinal layer nearer the cœlomic surface.

In Cœlomata and in many Cœlentera there are found distributed between the tracts of muscular tissue, bounding them and giving strength and consistency also to the walls of the body, of the alimentary canal, of the cœlom, and of the various organs and tissue-masses (such as nerve-centres, gonads, &c.) connected with these, tracts of tissue the function of which is skeletal. The SKELETAL TISSUE of Mollusca, in common with that of other Cœlomata, exhibits a wide range of minute structure, and is of differing density in various parts; it may be fibrous, membranous, or cartilaginous. The Mollusca, in common with the other Cœlomata, exhibit a remarkable kind of association between the various forms of skeletal tissue and the epithelium which lines the cœlomic cavity. The cœlomic cavity contains a liquid which is albuminous in chemical composition (BLOOD-LYMPH or HÆMOLYMPH), and into this liquid cells are shed from the cœlomic epithelium. They float therein and are known as BLOOD CORPUSCLES or LYMPH CORPUSCLES. The cœlomic space with its contained hæmolymph is not usually in Cœlomata, and is not in Mollusca, a simple even-walled cavity, but is broken up into numerous passages and recesses by the outgrowths, both of the alimentary canal and of its own walls. By the adhesion of its opposite walls, and by an irregularity in the process of increase of its area during growth, the cœlom becomes to a very large extent a spongy system of intercommunicating LACUNÆ or irregular spaces, filled with the cœlomic fluid. At the same time, the cœlomic space has a tendency to push its way in the form of narrow canals and sinuses between the layers of skeletal tissue, and thus to permeate together with the skeletal tissue in the form of a spongy, or it may be a tubular, network all the apparently solid portions of the animal body. This association of the nutritive and skeletal functions is accompanied by a complete identity of the tissues concerned in these functions. Not only is there complete gradation from one variety of skeletal tissue to another (*e.g.*, from membranous to fibrous, and from fibrous to cartilaginous) even in respect of the form of the cells and their intercellular substance, but the cœlomic epithelium, and consequently the hæmolymph with its floating corpuscles derived from that epithelium, is brought into the same continuity. The skeletal and blood-containing and -producing tissues in fact form one widely-varying but continuous whole, which may be called the SKELETO-TROPHIC SYSTEM OF TISSUES.

In many Cœlomata not only do the skeletal tissues allow the cœlomic space with its fluid and corpuscles to penetrate between their layers, but a special mode of extension of that space is found, which consists in the hollowing out of the solid substance of elongated cells having the form of fibres, which thus become tubular, and, admitting the nutritive fluid, serve as channels for its distribution. These are "capillary vessels," and it has yet to be shown that such are formed in the Mollusca. Larger vessels, however, concerned in guiding the movement of the cœlomic fluid in special directions are very usually developed in the Mollusca, as in other Cœlomata, by the growth of skeletal tissue around what are at first ill-defined extensions of the cœlomic space. In this way a portion of the cœlomic space becomes converted into vessels, whilst a large part remains with irregular walls extending in every direction between the skeletal tissues and freely communicating with the system of vessels. As in many other Cœlomata, muscular tissue grows around the largest vessel formed from the primitive cœlom, which thus becomes a contractile organ for propelling the blood-lymph fluid. This "HEART" has in Mollusca, as in most other Cœlomata in which it is developed, a dorsal position. A communication of the blood-lymph space with the exterior by means of a pore situated in the foot or elsewhere has been very generally asserted to be characteristic of Mollusca. It has been maintained that water is introduced by such a pore into the blood, or admitted into a special series of water-vessels. It has also been asserted that the blood-fluid is expelled by the Mollusca from these same pores. Recent investigation (**14**) has, however, made it probable that the pores are the pores of secreting glands, and do not lead into the vascular system. There is, it therefore appears, no admission or expulsion of water through such pores in connexion with the blood, although in some other Cœlomata it is established that water is taken into the cœlomic space through a pore (Echinoderms), whilst in some others there is no doubt that the cœlomic hæmolymph is occasionally discharged in quantity through pores of definite size and character (Earthworm, &c.).

We have thus seen that the Mollusca possess, in common with the other Cœlomata—1, a body composed of a vast *number of cells* or plastids, arranged so as to form a sac-like *body-wall*, and within that a second sac, the *met-enteron*, the wall of which is separated from the first by a *cœlom* or blood-lymph space; 2, a *stomodæum* and a *proctodæum*; 3, a *prostomium*, together with a differentiated *dorsal* and *ventral* surface, and consequently *right* and *left sides*, *i.e.*, bilateral symmetry; 4, a pair of *nephridia*; 5, *gonads* developed on the wall of the cœlom; 6, *deric* epithelium (producing horny and calcareous deposits on its surface), *enteric* epithelium, and *cœlomic* epithelium; 7, laterally paired masses of *nerve-tissue*, especially large in the prostomial region (nerve-centres or *ganglia*); 8, *muscular tissue*, forming a *somatic* tunic and a *splanchnic* tunic; 9, *skeleto-trophic tissues*, consisting of membranous, fibrous, and cartilaginous *supporting tissues*, and of *blood-vessels* and the walls of *blood-spaces*, the *cœlomic epithelium*, and the liquid tissue known as *hæmolymph* (commonly blood).

Schematic Mollusc.—Starting from this basis of structural features common to them and the rest of the Cœlomata, we may now point out what are the peculiar developments of structure which characterize the Mollusca and lead to the inference that they are members of one peculiar branch or phylum of the animal pedigree. In attempting thus to set forth the dominating structural attributes of a great group of organisms it is not possible to make use of arbitrary definitions. Of Mollusca, as of other great phyla, it is not possible categorically to enunciate a series of structural peculiarities which will be found to be true in reference to every member of the group. We have to remember that the process of adaptation in the course of long ages of development has removed in some cases one, in other cases another, of the original features characteristic of the ancestors from which the whole group may be supposed to have taken origin, and that it is possible (and actually is realized in fact) that some organisms may have lost all the *primary* characteristics of Molluscan organization, and yet be beyond all doubt definitely stamped as Mollusca by the retention of some *secondary* characteristic which is so peculiar as to prove their relationship with other Mollusca. An example in point is found in the curious fish-like form Phyllirhoë (fig. 58), which has none of the primary characteristics of a Mollusc, and yet is indisputably proved to belong to the Molluscan phylum by possessing the peculiar and elaborate lingual apparatus present in one branch of the phylum, the Glossophora.

In order to exhibit concisely the peculiarities of organization which characterize the Mollusca, we find it most convenient to construct a schematic Mollusc, which shall possess in an unexaggerated form the various structural arrangements which are more or less specialized, exaggerated, or even suppressed in particular members of the group. Such a schematic Mollusc is not to be regarded as an archetype, in the sense which has been attributed to that word, nor as the embodiment of an idea present to a creating mind, nor even as an epitome of developmental laws. Were knowledge sufficient, we should wish to make this schematic Mollusc the representation of the actual Molluscan ancestor from which the various living forms have sprung. To definitely claim for our schematic form any such significance in the present state of knowledge would be premature, but it may be taken as more or less coinciding with what we are justified, under present conditions, in picturing to ourselves as the original Mollusc or archi-Mollusc (more correctly Archimalakion). After describing this schematic form, we shall proceed to show how far it is realized or justified in each class and order of Mollusca successively.

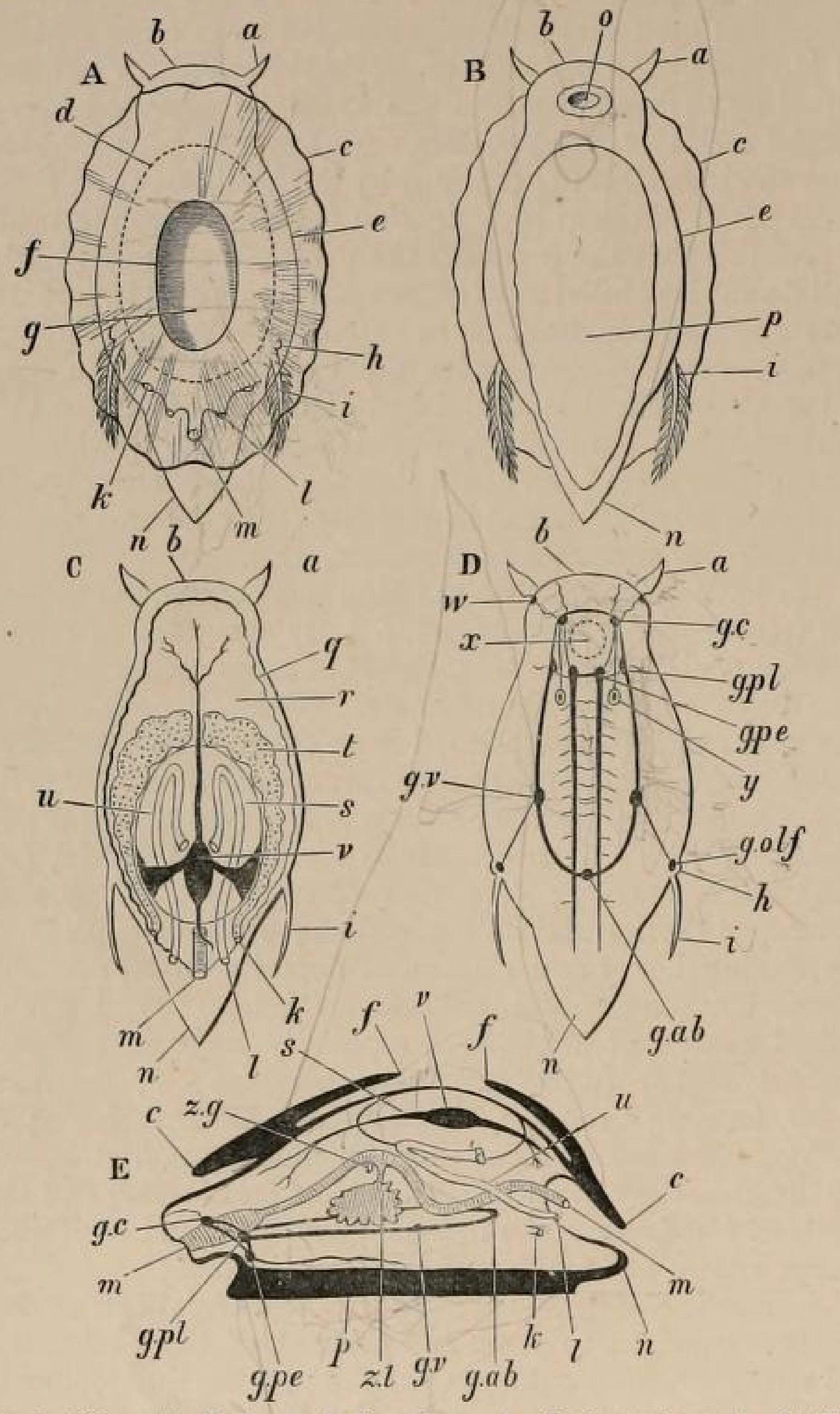

FIG. 1.—Schematic Mollusc. A. Dorsal aspect. B. Ventral aspect. C. The heart, pericardium, gonads, and nephridia shown in position. D. The nervous system; the reader is requested to note that the cord passing backwards from *g.pe* lies beneath, and does not in any way unite with the cord which passes from *g.ab* to *g.pl*. E. Diagram in which the body-wall is represented as cut in the median antero-posterior plane, so as to show organs in position,—the shell-sac is seen in section, but the shell is omitted.

Letters in all the figures as follows:—*a*, cephalic tentacle; *b*, head; *c*, edge of the mantle-skirt or limbus pallialis; *d*, dotted line indicating the line of origin of the free mantle-skirt from the sides of the visceral hump; *e*, outline of the foot seen through the mantle-skirt in A, which is supposed to be transparent, allowing the position of this and of the various parts *h*, *i*, *k*, *l*, *m*, to be seen through its substance; *f*, edge of the shell-follicle; *g*, the shell; *h*, the osphradium, paired (Spengel's olfactory organ); *i*, the ctenidium, paired (gill-plume); *k*, aperture of the gonad, paired; *l*, aperture of one of the two nephridia; *m*, anus; *n*, posterior region of the foot reaching farther back than the mass of viscera (dorsal hump) which it carries; *o*, mouth; *p*, plantar surface of the foot; *q*, cut edge of the body-wall of the dorsal region; *r*, cœlomic space (blood-lymph space or body-cavity), mostly occupied by liver, but to some extent retained as blood-channels and lacunæ; *s*, pericardial cavity; *t*, gonad (ovary or spermary), paired; *u*, nephridium, paired; *v*, ventricle of the heart receiving the right and the left auricles at its sides, and sending off anteriorly a large vessel, posteriorly a small one; *w*, the cephalic eye, paired; *x*, dotted ring to show the position occupied by the œsophagus in relation to the nerve ganglia and cords; *y*, the otocyst, paired; *z.l*, the digestive gland (so-called "liver") of the left side; *z.g*, duct of the digestive gland of the right side; *g.c*, cerebral ganglion united by the cerebral commissure to its fellow; *g.pl*, pleural ganglion united by the cerebro-pleural connective to the cerebral ganglion, and by the pleuro-pedal connective to the pedal ganglion; *g.pe*, the pedal ganglion united to its fellow by the pedal commissure—the two sending off posteriorly the long ladder-like pair of pedal nerves; *g.v*, the visceral ganglion (of the left side) united by the visceral loop or commissure to the similar ganglion on the right side, and by the viscero-pleural connective to the pleural ganglion; *g.ab*, abdominal ganglion developed on the course of the visceral loop; *g.olf*, olfactory ganglion placed near the osphradium on a nerve taking its origin from the visceral ganglion.

The schematic Mollusc (fig. 1, A to E) is oblong in shape, bilaterally symmetrical, with strongly differentiated dorsal and ventral surface, and has a well-marked HEAD, consisting of the prostomium (*b*) and the region immediately behind the mouth. Upon the head we place a pair of short CEPHALIC TENTACLES (*a*). The *mouth* is placed in the median line anteriorly, and is overhung by the prostomium (B, *o*); the *anus* is placed in the median line posteriorly, well raised on the dorsal surface (A, *m*). The apertures of a pair of NEPHRIDIA are seen in the neighbourhood of the anus right and left (A, *l*). Near the nephridial apertures, and in front of them, right and left, are the pair of apertures (*k*) appropriate to the ducts of the GONADS (generative pores).

The most permanent and distinctive Molluscan organ is the FOOT (Podium). This is formed by an excessive development of the somatic musculature along the ventral surface, distinctly ceasing at the region of the head, below which it suddenly projects as a powerful muscular mass (B, *p*; E, *p*). It may be compared, and is probably genetically identical, with the muscular ventral surface of the Planarians and with the suckers of Trematoda, but is more extensively developed than are those corresponding structures. The muscular tissue of the foot, and of all other parts of the body of all Mollusca, is cellular and unstriated, as distinguished from the composite muscular fibre (consisting of cell-fusions instead of separable cells) which occurs in Arthropoda and in Vertebrata, and which has the further distinction of being composed of alternating bands of substance of differing refractive power (hence "striated"). The appearance of cross striation seen in the muscular cells of some Molluscs (odontophore of Haliotis, Patella, &c.) requires further investigation. It is by no means altogether the same thing as the marking characteristic of striated muscular fibre.

Contrasting with the ventral foot is the thin-walled dorsal region of the body, which may be termed the antipodial region. This thin-walled region is formed by soft viscera covered in by the comparatively delicate and non-muscular body-wall (fig. 1, E). As the ventral foot is clearly separate from the projecting head, so is this dorsal region, and it is conveniently spoken of as the VISCERAL HUMP or "dome" (cupola). Protecting the visceral dome is a SHELL (conchylium) consisting of a horny basis impregnated with carbonate of lime,[1] and secreted by the deric epithelium of this region of the body (*g*). The shell in our schematic Mollusc is single, cap-shaped, and symmetrical. It does not lie entirely naked upon the surface of the visceral dome, but is embedded all round its margin, to a large extent in the body-wall. In fact, the integument of the visceral dome forms an open flattened sac in which the shell lies. This is the PRIMARY SHELL-SAC, or FOLLICLE (A and E, *f*). The wall of the body projects all round the visceral dome in the form of a flap or skirt, so as to overhang and conceal to some extent the head and the sides of the foot. This skirt, really an out-

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[1] As to the minute structure of the shell in various classes, see Carpenter's article "Shell" in the *Cyc'op. of Anat. and Physiol.* The limits of our space do not permit us to deal with this or other histological topics.

growth of the dorsal body-wall, is called the MANTLE-FLAP (limbus pallialis), or more shortly the MANTLE or PALLIUM (*c*). The space between the overhanging mantle-flap and the sides and neck of the animal which it overhangs is called the SUB-PALLIAL SPACE or CHAMBER. Posteriorly in this space are placed the anus and the pair of nephridial apertures (see fig. 1, E).

The development of the mantle-skirt and its sub-pallial space appears to have a causal relation, in the way of protection, to a pair of processes of the body-wall which spring, one on the right and one on the left, from the sides of the body, nearer the anus than the mouth, and are concealed by the mantle-flap to some extent (A, B, *i*). These processes have an axis in which are two blood-vessels, and are beset with two rows of flattened filaments, like the teeth of a comb in double series. These are the CTENIDIA or gill-combs. Usually, as will be seen in the sequel, they play the part of gills, but since in many Molluscs (Lamellibranchs) their function is not mainly respiratory, and since also other completely-formed gills are developed as special organs in some Molluscs to the exclusion of these processes, it is well not to speak of them simply as "gills" or "branchiæ," but to give them a non-physiological name such as that here proposed. Near the base of the stem of each ctenidium is a patch of the epithelium of the body-wall, peculiarly modified and supplied with a special nerve and ganglion. This is Spengel's olfactory organ, which tests the respiratory fluid, and is persistent in its position and nerve-supply throughout the group Mollusca. We propose to call it the OSPHRADIUM.

Passing now to the internal organs, our schematic Mollusc is found to possess an ALIMENTARY CANAL, which passes from mouth to anus in the middle line, leaving between it and the muscular body-wall a more or less spongy, in parts a spacious, CŒLOM. The *stomodæum* is large and muscular, the *proctodæum* short; the bulk of the alimentary canal is therefore developed from the metenteron or remnant of the arch-enteron after the cœlom has been pinched off from it. A paired outgrowth of the met-enteron forms the glandular diverticulum known as the digestive gland or (commonly) liver (E, *zg*, *zl*).

Dorsally to the alimentary tract the cœlom is spacious. The space (C, E, *s*) is termed the PERICARDIUM, since it is traversed by a vessel running fore and aft in the median line, which has contractile muscular walls and serves as a heart to propel the cœlomic blood-fluid. This pericardial space, although apparently derived from the original cœlom, is not in communication with the other spaces and blood-vessels derived from the cœlom; it never (or perhaps in a very few instances) contains in the adult the Molluscan blood or hæmolymph, and is always in free communication with the exterior through the tubes called *nephridia* (renal organs). The HEART receives symmetrically on each side, right and left, a dilated vessel bringing aerated blood from the ctenidia. These dilated vessels are termed the *auricles of the heart*, whilst the median portion itself, at the point where these vessels join it, is termed the *ventricle of the heart* (C, *v*). The vessel passing fore and aft from the ventricle gives off a few trunks which open into spaces of the cœlom, the so-called lacunæ; these are excavated in every direction between the viscera and the various bundles of fibrous and muscular tissue, and may assume more or less the character of tube-like vessels with definite walls. Right and left opening into the pericardial cœlom is a coiled tube, the farther extremity of which opens to the exterior by the side of the anus. These two tubes (C, *u*) are the symmetrically disposed NEPHRIDIA (renal organs).

The GONADS (ovaries or spermaries) are placed in the mid-dorsal region of the cœlom (C, *t*), and have their own apertures in the immediate neighbourhood of those of the nephridia. The apertures are paired right and left, and so are the ducts into which they lead; but at present we have no ground for determining whether the gonad itself was primarily in Molluscs a paired organ or a median organ, nor have we any well-founded conception as to the nature of the ducts when present, and their original relationship to the gonads. The genital ducts of some organisms are modified nephridia, but the nature of those of Mollusca, of Arthropoda, of Echinoderma, of Nematoidea, and of some Vertebrata has yet to be elucidated.

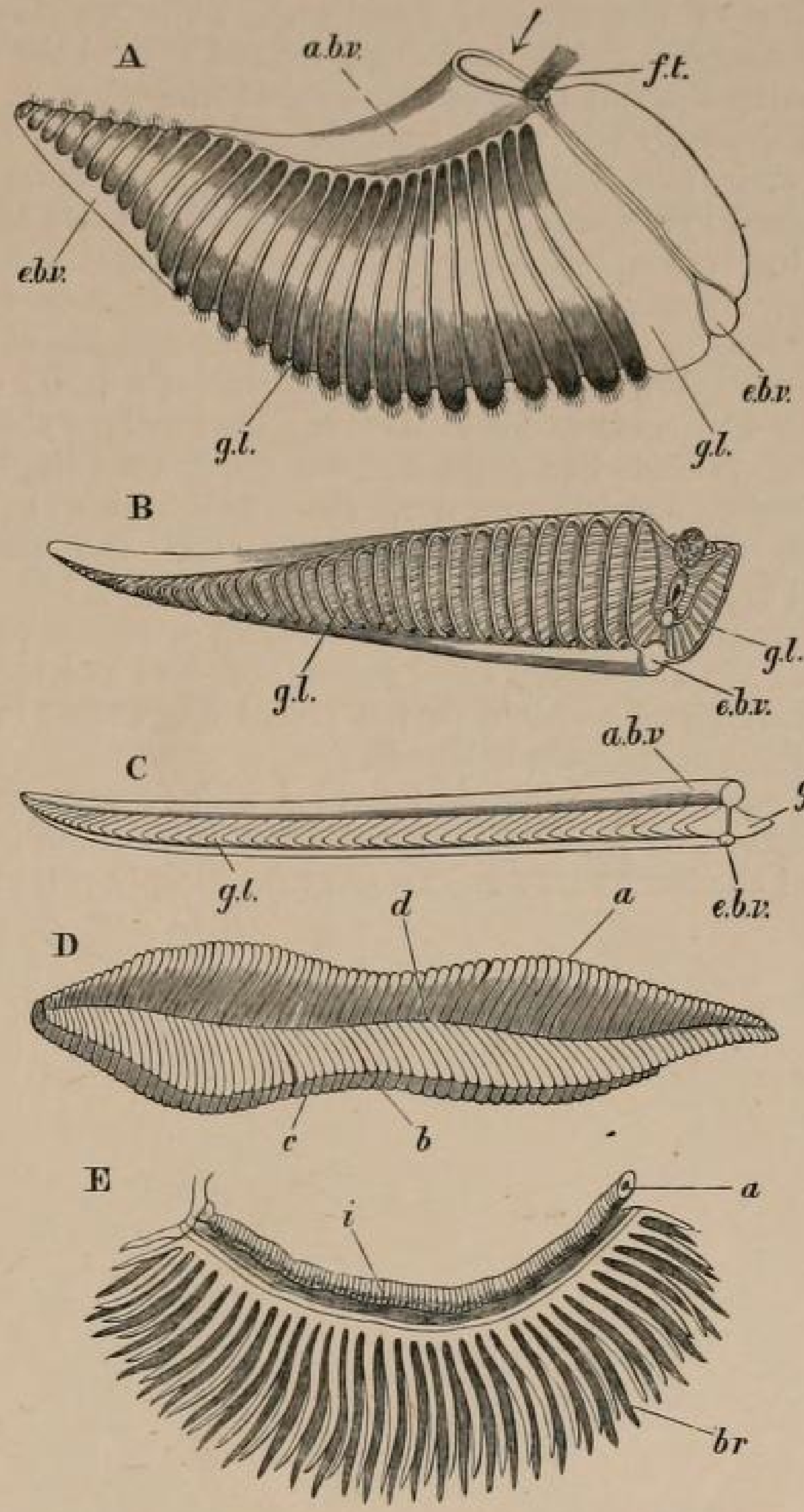


FIG. 2.—Ctenidia of various Mollusca (original). A. Of Chiton; *f.t.*, fibrous tissue; *a.b.v.*, afferent blood-vessel; *e.b.v.*, efferent blood-vessel; *g.l.*, laterally paired lamellæ. B. Of Sepia; letters as in A. C. Of Fissurella; letters as in A. D. Of Nucula; *d*, position of axis with blood-vessels; *a*, inner; *b* and *c*, outer row of lamellæ. E. Of Paludina; *i*, intestine running parallel with the axis of the ctenidium and ending in the anus *a*; *br*, rows of elongate processes corresponding to the two series of lamellæ of the upper figures.

The disposition of the nerve-centres is highly characteristic. There are four long cords composed of both nerve-fibres and nerve-cells which are disposed in pairs, two right and left of the pedal area or foot, two more dorsally and tending to a deeper position than that occupied by the pedal cords, so as to lie freely within the cœlomic space unattached to the body-wall. These are respectively the PEDAL NERVE-CORDS and the VISCERAL NERVE-CORDS. The latter meet and join one another posteriorly. A right and left (D, *g.v*), and a median abdominal (*g.ab*) ganglion are placed on these cords, and from them are given off the osphradial nerves which have special ganglia (*g.olf*). In the region of the prostomium the pedal nerve-cords are enlarged behind the mouth, forming the *pedal ganglia* (*g.pe*), and are united by nerve-fibres to one another. From this spot they are continued forward into the prostomium, where they enlarge to form the right and left *cerebral ganglia* (*g.c*), which are united to one another by nerve-fibres in front of the mouth, just as the pedal ganglia are behind it. The right and left pedal ganglia are joined by transverse cords to the right and left visceral cords respectively, the point of union being marked on either side by a swelling (*g.pl*) known as the pleural ganglion. The visceral nerve-cord can also be traced up on each side beyond the pleural ganglion to the cerebral ganglion. Thus we have a nearly complete double nerve-ring formed around the œsophagus by the two pairs of nerve-cords which are in this region drawn, as it were, towards each other and away from their lateral position both behind and before the stomodæal invagination. Whilst the swollen parts of the nerve-tracts are termed *ganglia*, the connecting cords are conveniently distinguished either as *connectives* or as *commissures*. Commissures connect two ganglia of the same pair We have a cerebral commissure, a pedal commissure and a visceral commissure. Connectives connect ganglia of dissimilar pairs, and we speak accordingly of the cerebro-pedal connective, the cerebro-pleural connective, the pleuro-pedal connective, and the viscero-pleural connective.

An ENTERIC NERVOUS SYSTEM forming a plexus on the walls of the alimentary canal exists, but does not exhibit cords and ganglia visible to the naked eye except in the large Dibranchiate Cephalopods.

Our schematic Mollusc is provided with certain ORGANS OF SPECIAL SENSE. Tactile organs occur on the head in the form of short CEPHALIC TENTACLES (*a*). Deeply placed are a pair of closed vesicles containing each a calcareous concretion and acting as auditory organs; these are known as OCTOCYSTS (D, *y*). They are situated behind the mouth in the foremost portion of the foot. At the base of each cephalic tentacle is a pigmented eye-spot—the CEPHALIC EYE (D, *w*). The OSPHRADIUM (*h*), or peculiar patch of olfactory epithelium at the base of the ctenidium, has already been mentioned.

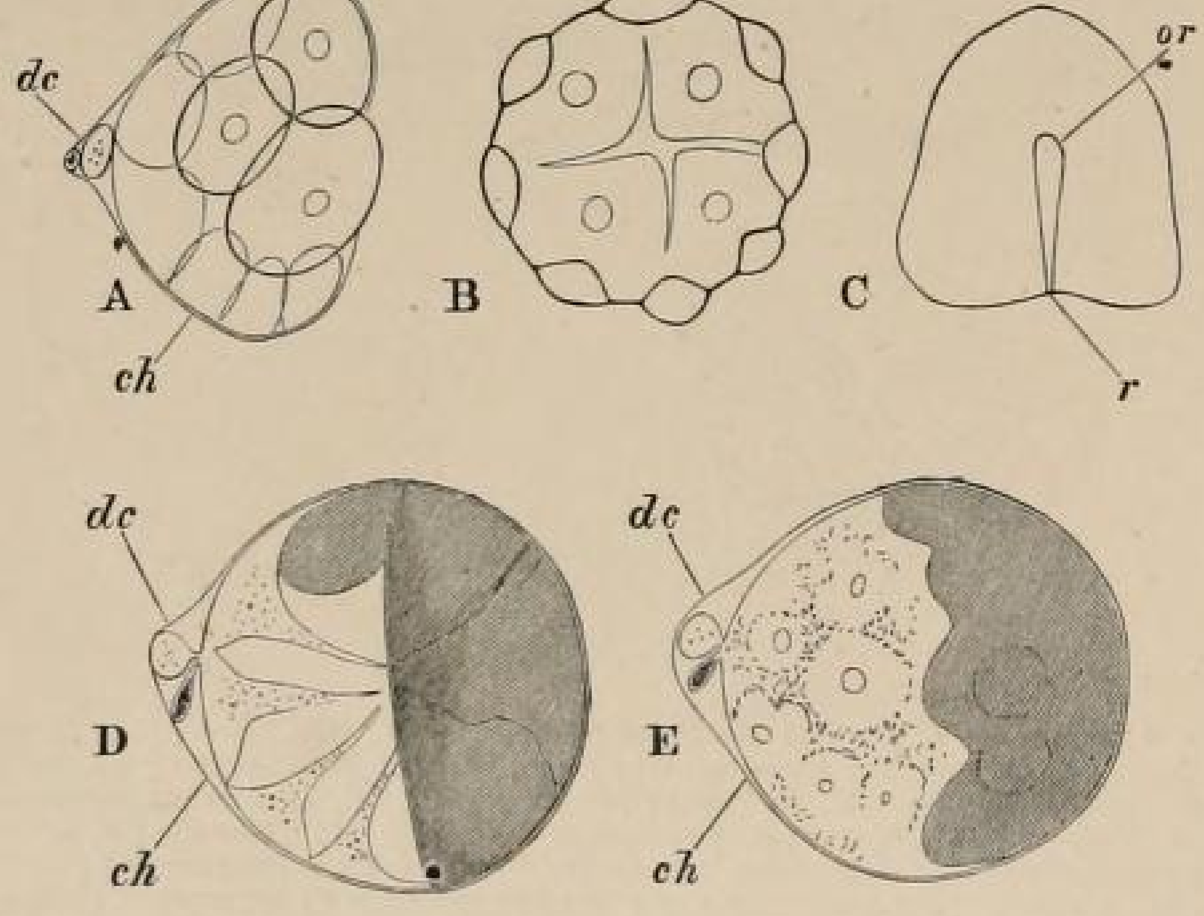


FIG. 3.—Development of the Pond-Snail, *Limnæus stagnalis* (after Lankester, 15). *dc*, directive corpuscles (præseminal outcast cells); *ch*, egg-envelope or chorion; *or*, oral end of the blastopore; *r*, anal end of the blastopore. A. Formation of the Diblastula by the invagination of larger cells into the area of smaller cells (optical section). B. View of the same specimen from the surface of invagination; the smaller cells are seen at the periphery; by division they will multiply and extend themselves over the four larger cells. C. Fully-formed Diblastula, surface view to show the elongated form of the orifice of invagination or blastopore; its middle portion closes up and coincides with the region of the foot; the extremity, *or*, coincides with the mouth and stomodæum, the opposite extremity, *r*, with the anus. D. Optical section of an embryo a little older than A. E. Surface view of the same embryo.

To the scheme thus exhibited of the possible organization of the ancestral Mollusc we shall now add a sketch of the mode in which this form of body and series of internal organs are developed from the egg.

The egg-cell of Mollusca is either free from food material—a simple protoplasmic corpuscle—or charged with food material to a greater or less extent. Those cases which appear to be most typical—that is to say, which adhere to a procedure which was probably common at one time to all then existing Mollusca, and which has been departed from only in later and special lines of descent—show approxi-

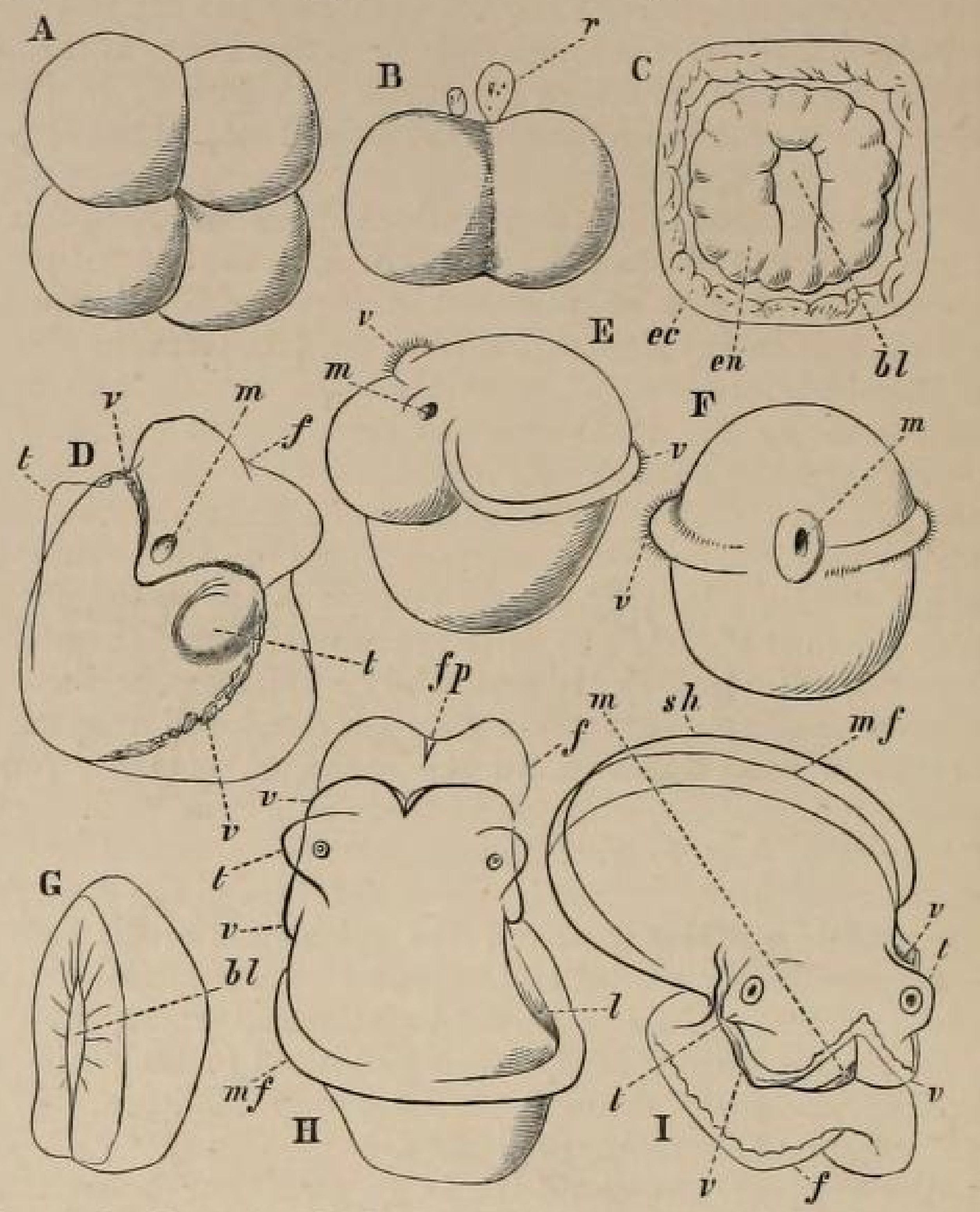


FIG. 4.—Development of the Pond-Snail, *Limnæus stagnalis* (after Lankester, 15). *r*, directive corpuscle; *bl*, blastopore; *en*, endoderm or enteric cell layer; *ec*, ectoderm or deric cell-layer; *v*, velum; *m*, mouth; *f*, foot; *t*, tentacles; *fp*, pore in the foot (belonging to the pedal gland?); *mf*, the mantle-flap or limbus pallialis; *sh*, the shell; *l*, the sub-pallial space, here destined to become the lung. A. First four cells resulting from the cleavage of the original egg-cell. B. Side view of the same. C. Diblastula stage (see fig. 3), showing the two cell-layers and the blastopore. D, E, F. Trochosphere stage, D older than E or F. G. Three-quarter view of a Diblastula, to show the orifice of invagination of the endoderm or blastopore, *bl*. H, I. Veliger stage later than D. (Compare fig. 70 and fig. 72***).

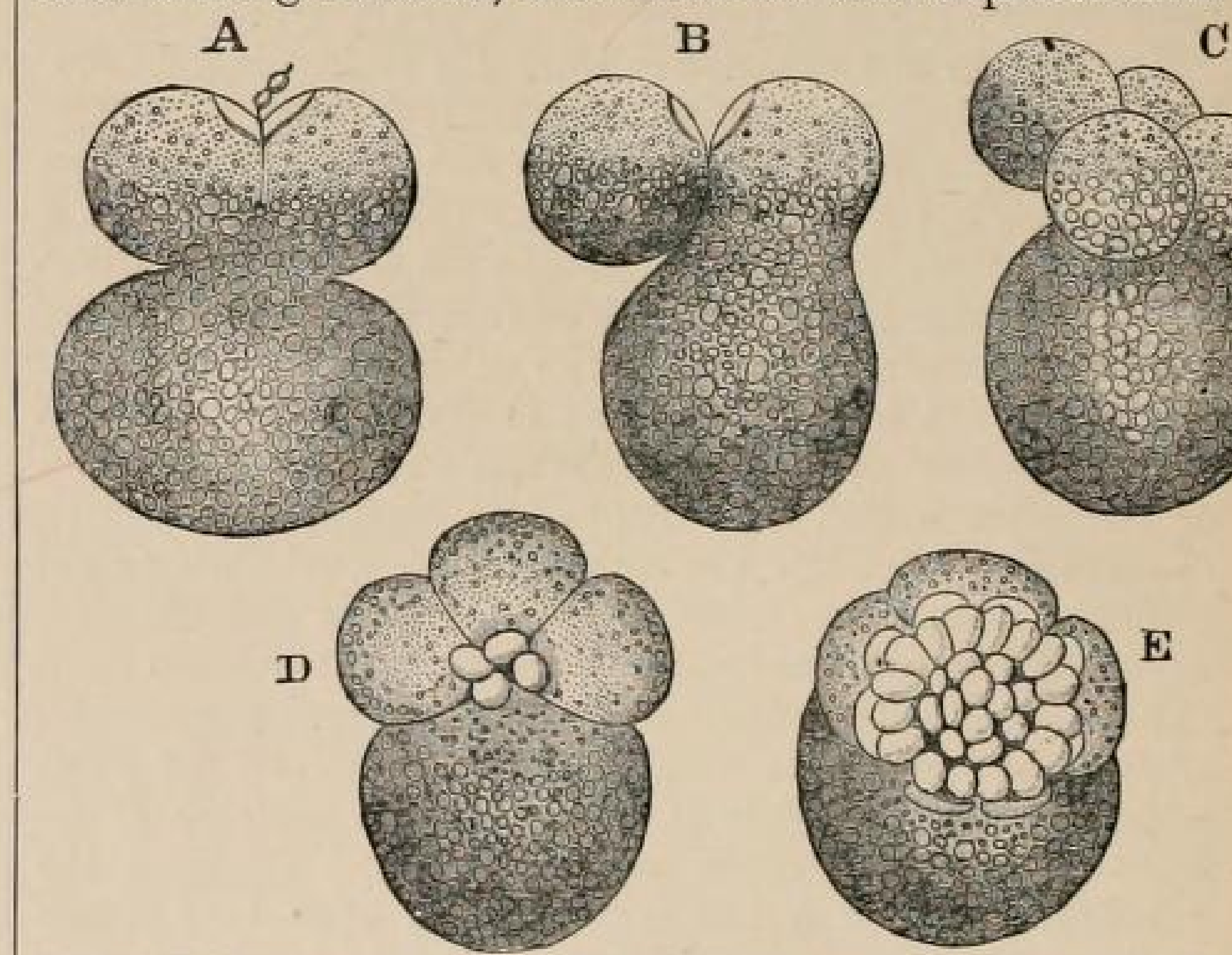


FIG. 5.—Early stages of division of the fertilized egg-cell in *Nassa mutabilis* (from Balfour, after Bobretzky). A. The egg-cell has divided into two spheres, of which the lower contains more food-material, whilst the upper is again incompletely divided into two smaller spheres. Resting on the dividing upper sphere are the eight-shaped "directive corpuscles," better called "præseminal outcast cells or apoblasts," since they are the result of a cell-division which affects the egg-cell before it is impregnated, and are mere refuse, destined to disappear. B. One of the two smaller spheres is reunited to the larger sphere. C. The single small sphere has divided into two, and the reunited mass has divided into two, of which one is oblong and practically double, as in B. D. Each of the four segment-cells gives rise by division to a small pellucid cell. E. The cap of small cells has increased in number by repeated formation of pellucid cells in the same way, and by division of those first formed. The cap will spread over and enclose the four segment-cells, as in fig. 3, A, B.

mately the following history. By division of the egg-cell (fig. 3, A, B; fig. 4, A, B; and fig. 5) a mulberry-mass of embryonic-cells is formed (Morula), which dilates, forming a one-cell-layered sac (Blastula). By invagination one portion of this sphere becomes tucked into the other—as in the preparation of a woven night-cap for the head (fig. 6, B; fig. 7, A). The orifice of invagination (blastopore) narrows, and we now have a two-cell-layered sac,—the Diblastula. The invaginated layer is the enteric cell-layer or endoderm; the outer cell-layer is the deric cell-layer or ectoderm. The cavity communicating with the blastopore and lined by the endoderm is the arch-enteron. The blastopore, together with the whole embryo, now elongates. The blastopore then closes along the middle portion of its extent, which corresponds with the later developed foot. At the same time the stomodæum or oral invagination forms around the anterior remnant of the blastopore, and the proctodæum or anal invagination forms around the posterior remnant of the blastopore. There are, however, variations in regard to the relation of the blastopore to the mouth and to the anus which are probably modifications of the original process described above. An examination of figs. 3, 4, 5, 6, 7, and of others illustrative of the embryology of particular forms which occur later in this article, is now recommended to the reader. The explanation of the figures has been made very full so as to avoid the necessity of special descriptions in the text. Internally, by the nipping off of a pair of lateral outgrowths (forming part of the indefinable "mesoblast") from the enteric cell-layer the foundations of the cœlomic cavity are laid. In some Cœlomata these outgrowths are hollow and of large size. In Mollusca they are not hollow and large, which is probably the archaic condition, but they consist at first of a few cells only, adherent to one another; these cells then diverge, applying themselves to the body-wall and to the gut-wall so as to form the lining layer of the cœlomic cavity. Muscular tissue develops from deep-lying cells, and the rudiments of the paired nerve-tracts from thickenings of the deric-cell layer or ectoderm.

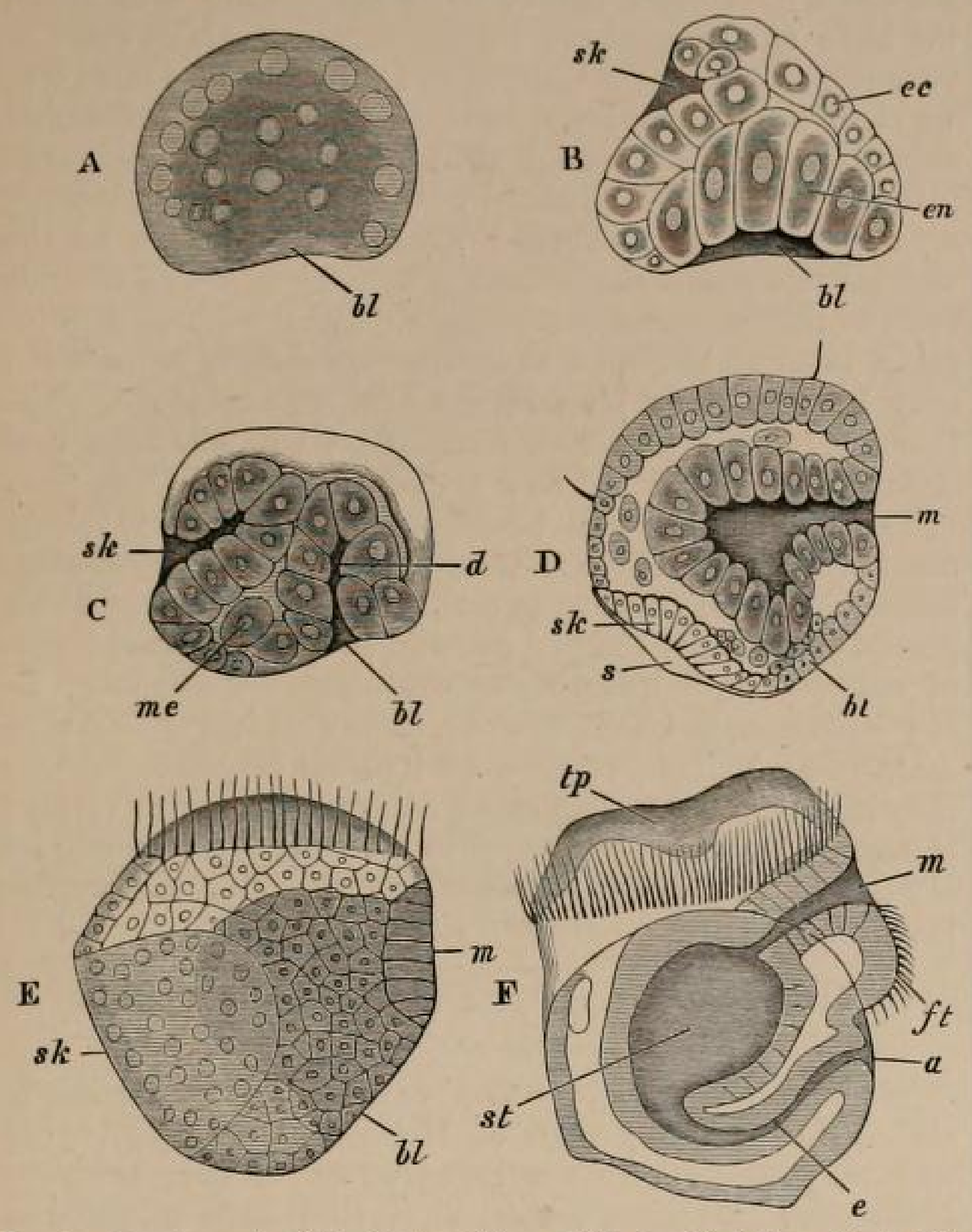


Fig. 6.—Development of the Oyster, *Ostrea edulis* (modified from Horst, 16). A. Blastula stage (one-cell-layered sac), with commencing invagination of the wall of the sac at *bl*, the blastopore. B. Optical section of a somewhat later stage, in which a second invagination has commenced—namely, that of the shell-gland *sk*; *bl*, blastopore; *en*, invaginated endoderm (wall of the future arch-enteron); *ec*, ectoderm. C. Similar optical section at a little later stage. The invagination connected with the blastopore is now more contracted, *d*; and cells, *me*, forming the mesoblast from which the cœlom and muscular and skeleto-trophic tissues develop, are separated. D. Similar section of a later stage. The blastopore, *bl*, has closed; the anus will subsequently perforate the corresponding area. A new aperture, *m*, the mouth, has eaten its way into the invaginated endodermal sac, and the cells pushed in with it constitute the stomodæum. The shell-gland, *sk*, is flattened out, and a delicate shell, *s*, appears on its surface. The ciliated velar ring is cut in the section, as shown by the two projecting cilia on the upper part of the figure. The embryo is now a Trochosphere. E. Surface view of an embryo at a period almost identical with that of D. F. Later embryo seen as a transparent object. *m*, mouth; *ft*, foot; *a*, anus; *e*, intestine; *st*, stomach; *tp*, velar area of the prostomium. The extent of the shell and commencing upgrowth of the mantle-skirt is indicated by a line forming a curve from *a* to F.

N.B.—In this development, as in that of Pisidium (figs. 150, 151), no part of the blastopore persists either as mouth or as anus, but the aperture closes,—the pedicle of invagination, or narrow neck of the invaginated arch-enteron, becoming the intestine. The mouth and the anus are formed as independent in-pushings, the mouth with stomodæum first, and the short anal proctodæum much later. This interpretation of the appearances is contrary to that of Horst (16), from whom our drawings of the oyster's development are taken. The account given by the American naturalist Brooks (19) differs greatly as to matter of fact from that of Horst, and appears to be erroneous in some respects.

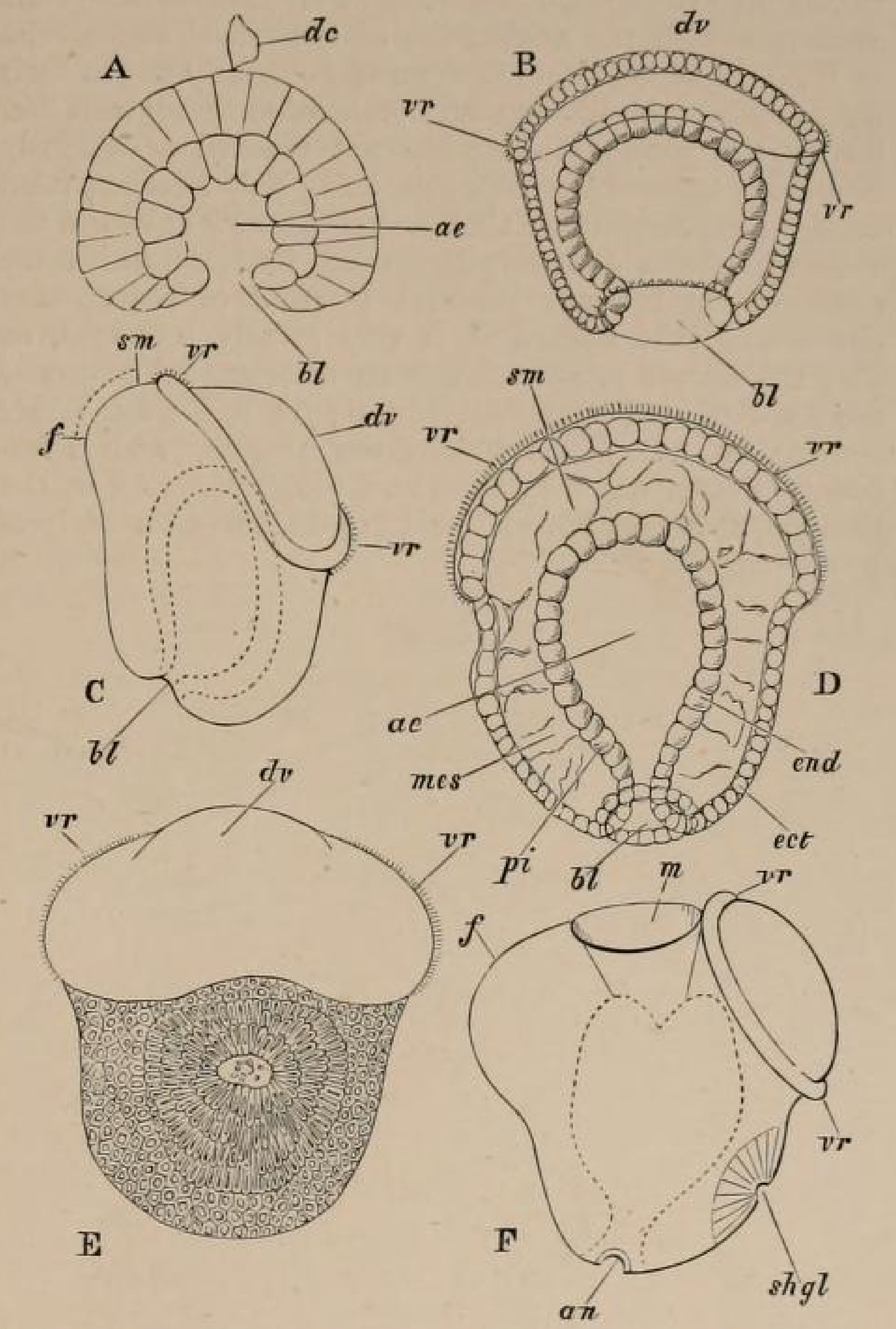


Fig. 7.—Development of the River-Snail, *Paludina vivipara* (after Lankester, 17). *dc*, directive corpuscle (outcast cell); *ae*, arch-enteron or cavity lined by the enteric cell-layer or endoderm; *bl*, blastopore; *vr*, velum or circlet of ciliated cells; *dv*, velar area or cephalic dome; *sm*, site of the as yet unformed mouth; *f*, foot; *mes*, rudiments of the skeleto-trophic tissues; *pi*, the pedicle of invagination, the future rectum; *shgl*, the primitive shell-sac or shell-gland; *m*, mouth; *an*, anus. A. Diblastula phase (optical section). B. The Diblastula has become a Trochosphere by the development of the ciliated ring *vr* (optical section). C. Side view of the Trochosphere with commencing formation of the foot. D. Further advanced Trochosphere (optical section). E. The Trochosphere passing to the Veliger stage, dorsal view showing the formation of the primitive shell-sac. F. Side view of the same, showing foot, shell-sac (*shgl*), velum (*vr*), mouth, and anus.

N.B.—In this development the blastopore is not elongated; it persists as the anus. The mouth and stomodæum form independently of the blastopore.

The external form meanwhile passes through highly characteristic changes, which are on the whole fairly constant throughout the Mollusca. A circlet of cilia forms when the embryo is still nearly spherical (fig. 4, F; fig. 6, E; fig. 7, B), in an equatorial position. As growth proceeds, one hemisphere remains relatively small, the other elongates and enlarges. Both mouth and anus are placed in the larger area; the smaller area is the prostomium simply; the ciliated band is therefore in front of the mouth. The larval form thus produced is known as the Trochosphere. It exactly agrees with the larval form of many Chætopod worms and other Cœlomata. Most remarkable is its agreement with the adult form of the Wheel animalcules or Rotifera, which retain the præ-oral ciliated band as their chief organ of locomotion and prehension throughout life. So far the young Mollusc has not reached a definitely Molluscan stage of development, being only in a condition common to it and other Cœlomata. It now passes to the veliger phase, a definitely Molluscan form, in which the disproportion between the area in front of the ciliated circlet and that behind it is very greatly increased, so that the former is now simply an emarginated region of the head fringed with cilia (fig. 8; fig. 6, F; fig. 7, F; and fig. 60, A). It is termed the "velum," and is frequently drawn out into lobes and processes. As in the Rotifera, it serves the veliger larva as an organ of locomotion. In a very few Molluscs, but notably in the Common Pond-Snail, the emarginated bilobed velum is retained in full proportions in adult life (fig. 70), having lost its marginal fringe of specially long cilia and its locomotor function. The body of the Veliger is characterized by the development of the visceral hump on one surface, and by that of the foot on the other. Growth is greater in the vertical dorso-ventral axis than in the longitudinal oro-anal axis; consequently the foot is relatively small and projects as a blunt process between mouth and anus, which are not widely distant from one another, whilst the antipedal area projects in the form of a great hump or dome. In the centre of this antipedal area there has appeared (often at a very early period) a gland-like depression or follicle of the integument (fig. 6, C, *sk*; fig. 7, E, F, *shgl*; fig. 60, B; fig. 68, *shs*; fig. 72***, *ss*). This is the primitive shell-sac discovered by Lankester (**18**) in 1871, and shown by him to precede the development of the permanent shell in a variety of Molluscan types. The cavity of this small sac becomes filled by a horny substance, and then it very usually disappears, whilst a delicate shell, commencing from this spot as a centre, forms and spreads upon the surface of the visceral dome.

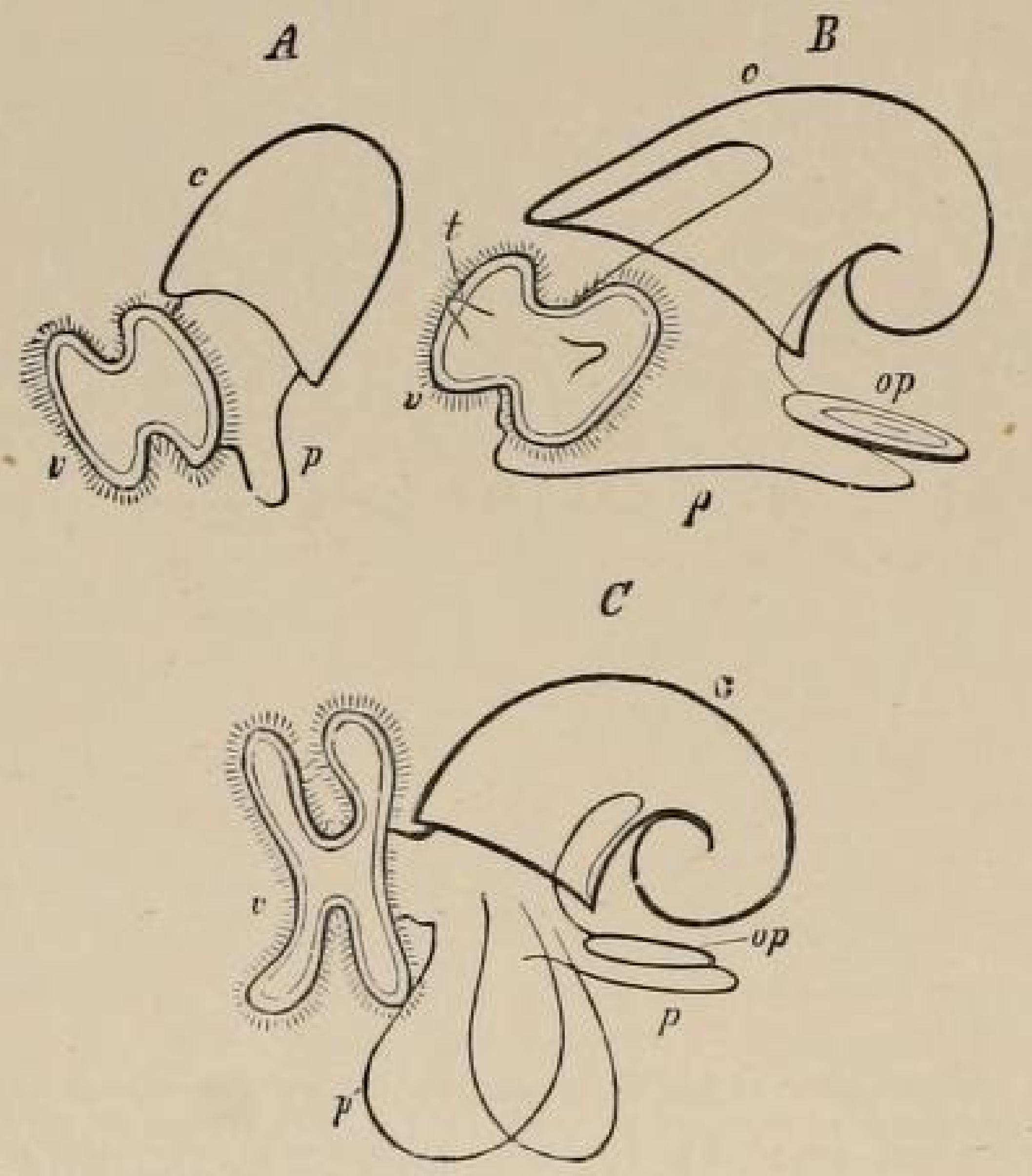


FIG. 8.—"Veliger" embryonic form of Mollusca (from Gegenbaur). *v*, velum; *c*, visceral dome with dependent mantle-skirt; *p*, foot; *t*, cephalic tentacles; *op*, operculum. A. Earlier, and B, later, Veliger of a Gastropod. C. Veliger of a Pteropod showing lobe-like processes of the velum and the great paired outgrowths of the foot.

The embryonic shell-sac or shell-gland represents in a transient form, in the individual development of most Mollusca, that condition of the shell-forming area which we have sketched above in the schematic Mollusc. In very few instances (in Chiton, and probably in Limax), as we shall see below, the *primitive shell-sac* is retained and enlarged as the permanent shell-forming area. It is supplanted in other Molluscs by a *secondary shell-forming area*, namely, that afforded by the free surface of the visceral hump, the shell-forming activity of which extends even to the surface of the depending mantle-skirt. Accordingly, in most Mollusca the *primitive shell* is represented only by the horny plug of the primitive shell-sac. The permanent shell is a new formation on a new area, and should be distinguished as a *secondary shell.*

The ctenidia, it will be observed, have not yet been mentioned, and they are indeed the last of the characteristic Molluscan organs to make their appearance. Their possible relation to the præ-oral and post-oral ciliated bands of embryos similar to the Trochosphere are discussed by the writer in the *Quart. Jour. Micr. Sci.*, vol. xvii. p. 423. The Veliger, as soon as its shell begins to assume definite shape, is no longer of a form common to various classes of Mollusca, but acquires characters peculiar to its class. At this point, therefore, we shall for the present leave it.

Systematic Review of the Classes and Orders of Mollusca.

We are now in a position to pass systematically in review the various groups of Mollusca, showing in what way they conform to the organization of our schematic Mollusc, and in what special ways they have modified or even suppressed parts present in it, or phases in the representative embryonic history which has just been sketched. It will be found that the foot, the shell, the mantle-skirt, and the ctenidia, undergo the most remarkable changes of form and proportionate development in the various classes —changes which are correlated with extreme changes and elaboration in the respective functions of those parts.

Division of the Phylum into two Branches.—The Mollusca are sharply divided into two great lines of descent or branches, according as the prostomial region is atrophied on the one hand, or largely developed on the other.

The probabilities are in favour of any ancestral form—the hypothetical archi-Mollusc which connected the Mollusca with their non-Molluscan forefathers—having possessed, as do all the more primitive forms of Cœlomata, a well-marked prostomium, and consequently a head. The one series of Mollusca descended from the primitive head-bearing Molluscs have acquired an organization in which the Molluscan characteristics have become modified in definite relation to a sessile inactive life. As the most prominent result of the adaptation to such sessile life they exhibit an atrophy of the cephalic region. They form the branch LIPOCEPHALA—the mussels, oysters, cockles, and clams. The other series have retained an active, in many cases a highly aggressive, mode of life; they have, correspondingly, not only retained a well-developed head, but have developed a special aggressive organ in connexion with the mouth, which, on account of its remarkable nature and the peculiarities of the details of its mechanism, serves to indicate a very close genetic connexion between all such animals as possess it. This remarkable organ is the odontophore, consisting of a lingual ribbon, rasp, or radula, with its cushion and muscles. On account of the possession of this organ this great branch of the Molluscan phylum may be best designated GLOSSOPHORA. Any term which merely points to the possession of a head is objectionable, since this is common to them and the hypothetical archi-Mollusca from which they descend. The term Odontophora, which has been applied to them, is also unsuitable, since the organ which characterizes them is not a tooth, but a tongue.

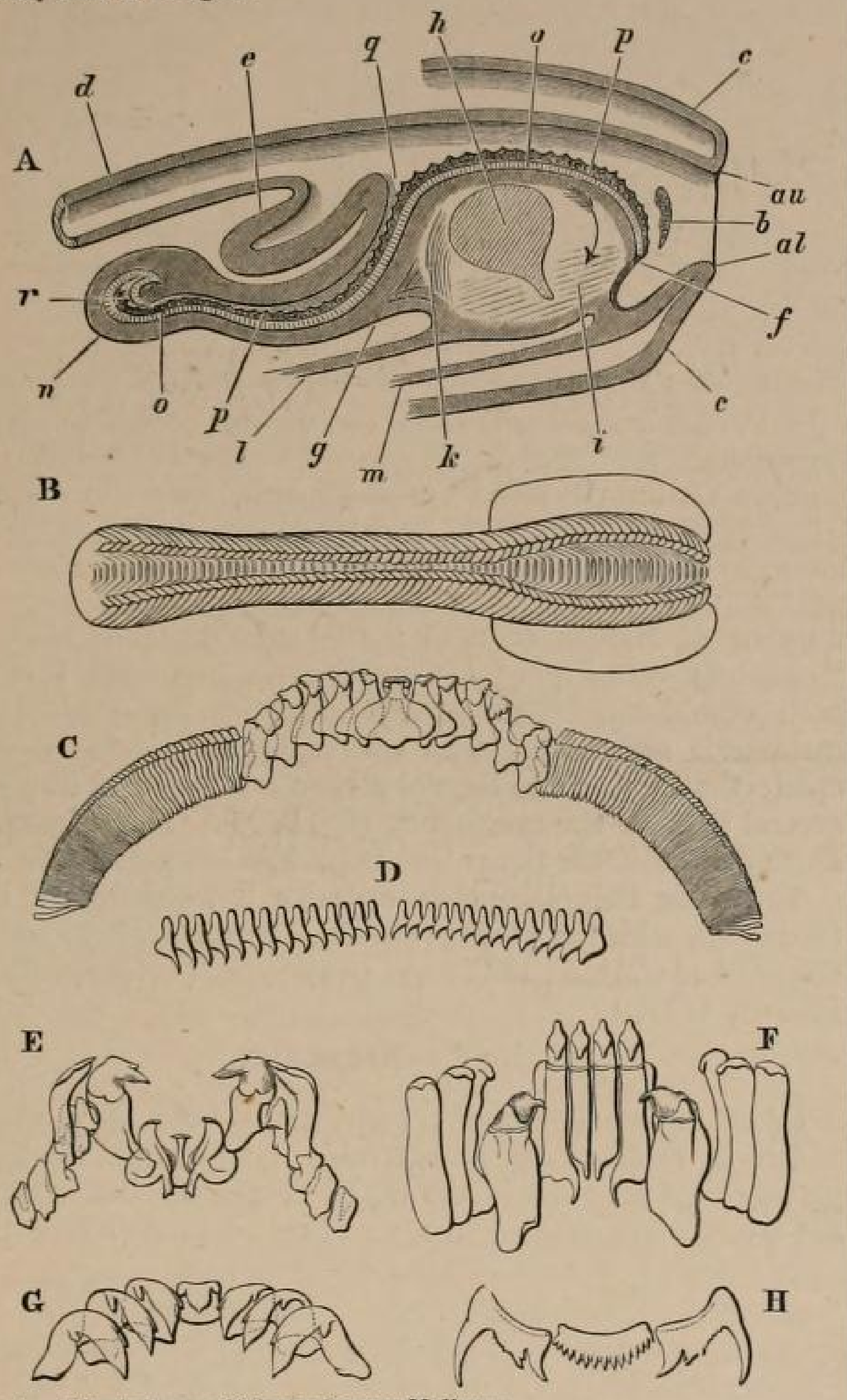


FIG. 9.—Odontophore of Glossophorous Mollusca.

A. Diagram showing mouth, œsophagus, and lingual apparatus of a Gastropod in section. *au*, upper lip; *al*, lower lip; *b*, calcareo-corneous jaw of left side; *c*, outer surface of the snout; *d*, œsophagus; *e*, fold in the wall of the œsophagus behind the radular sac (*n*); *f*, anterior termination of the radula and its bed, the point at which it wears away; *g*, base of the radular sac or recess of the pharynx; *h*, cartilaginous piece developed in the floor of the pharynx beneath the radula, and serving for the attachment of numerous muscles, and for the support of the radula; *i*, anterior muscles; *k*, posterior muscles attached to the cartilage; *l*, muscle acting as a retractor of the buccal mass; *m*, muscle attached to the lower lip; *n*, posterior extremity of the radular sac; *o*, the bed of the radula or layer of cells by which its lower surface is formed; *p*, the horny radula or lingual ribbon; *q*, opening of the radular sac into the pharynx or buccal cavity; *r*, cells at the extreme end of the inner surface of the radular sac which produce as a "cuticular secretion" the rows of teeth of the upper surface of the radula.

B. Radula or lingual ribbon of *Paludina vivipara*, stripped from its bed,—a horny, cuticular product.

C. A single row of teeth from the radula of *Trochus cinerarius*. Rhipidoglossate; formula, x.5.1.5.x.

D. A single row of teeth from the radula of *Faultima fragilis*. Ptenoglossate; formula, x.0.x.

E. A single row of teeth from the radula of *Chiton cinereus*. Too elaborate for formulation.

F. A single row of teeth from the radula of *Patella vulgata*. Formula, 3.1.4.1.3.

G. A single row of teeth from the radula of *Cypræa helvola*. Tænioglossate; formula, 3.1.3.

H. A single row of teeth from the radula of *Nassa annulata*. Rachiglossate; formula, 1.1.1. The Common Whelk is similar to this.

The general structure of the odontophore (= tooth-bearer, in allusion to the rasp-like ribbon) of the glossophorous Mollusca may be conveniently described at once. Essentially it is a tube-like outgrowth—the *radular sac* (fig. 9, A, *g*, *n*)—in the median line of the ventral floor of the stomodæum, upon the inner surface of which is formed a chitinous band (the radula) beset with minute teeth like a rasp (*p*). Anteriorly the ventral wall of the diverticulum is converted into cartilage (*h*), to which protractor and retractor muscles are attached (*k*, *i*), so that by the action of the former the cartilage, with the anterior end of the ribbon resting firmly upon it, may be brought forward into the space between the lips of the oral aperture (*au*, *al*), and made to exert there a backward and forward rasping action by the alternate contraction of retractor and protractor muscles attached to the cartilage. But in many Glossophora (*e.g.*, the Whelk) the apparatus is complicated by the fact that the diverticulum itself, with its contained radula, rests but loosely on the cartilage, and has special muscles attached to each end of it, arising from the body wall; these muscles pull the whole diverticulum or radular sac alternately backwards and forwards over the surface of the cartilage. This action, which is quite distinct from the movement of the cartilage itself, may be witnessed in a Whelk if the pharynx be opened whilst it is alive. It has also been seen in living transparent Gastropods. The chitinous ribbon is continuously growing forward from the tube-like diverticulum as a finger-nail does on its bed, and thus the wearing away of the part which rests on the cartilage and is brought into active use, is made up for by the advance of the ribbon in the same way as the wearing down of the finger-nail is counterbalanced by its own forward growth. And, just as the new substance of the finger-nail is formed in the concealed part, sunk posteriorly below a fold of skin, and yet is continually carried forward with the forward movement of the bed on which it rests, and which forms its undermost layers, so is the new substance of the radula formed in the compressed extremity of the radular sac (*n*), and carried forward by the forward movement of the bed (*o*) on which it rests, and by which is formed its undermost layer. This forward-moving bed is not merely the ventral wall of the radular diverticulum, but includes also that portion of the floor of the oral cavity to which the radula adheres (as far forward as the point *f* in fig. 9, A). At the spot where the radula ceases, the forward growth-movement of the floor also ceases, just as in the case of the finger-nail the similar growth-movement ceases at the line where the nail becomes free.

The radula or cuticular product of the slowly-moving bed can be stripped off, and is then found to consist of a ribbon-like area, upon which are set numerous tooth-like processes of various form in transverse rows, which follow one another closely, and exactly resemble one another in the form of their teeth (fig. 9, B). The tooth-like processes in a single transverse row are of very different shape and number in different members of the Glossophora, and it is possible to use a formula for their description. Thus, when in each row there is a single median tooth with three teeth on each side of it more or less closely resembling one another, as in fig. 9, G, we write the formula 3.1.3. When there are additional lateral pieces of a different shape to those immediately adjoining the central tooth, we indicate them by the figure 0, repeated to represent their number, thus 0000.1.1.1.0000 is the formula for the lingual teeth of *Chiton Stelleri*. A single median tooth, an admedian series, and a lateral series may be thus distinguished. In some Glossophora only median teeth are present, or large median teeth with a single small admedian tooth on each side of it (fig. 9, H); these are termed Rachiglossa (formula, —.1.— or 1.1.1). In a large number of Glossophora we have three admedian on each side and one median, no lateral pieces (fig. 9, G); these are termed Tænioglossa (formula, 3.1.3). Those with numerous lateral pieces, four to six or more admedian pieces, and a median piece or tooth (fig. 9, C) are termed Rhipidoglossa (formula, x.6.1.6.x, where x stands for an indefinite number of lateral pieces). The Toxoglossa have

1.0.1, the central tooth being absent and the lateral teeth peculiarly long and connected with muscles. The term Ptenoglossa (fig. 9, D) is applied to those Glossophora in which the radula presents no median tooth, but an indefinite and large number of admedian teeth, giving the formula x.0.x. When the admedian teeth are indefinite (forty to fifty), and a median tooth is present, the term Myriaglossa is applied (formula, x.1.x). It must be understood that the pieces or teeth thus formulated may themselves vary much in form, being either flat plates, or denticulated, hooked, or spine-like bodies. We shall revert to the terms thus explained in the systematic descriptions of the groups of Glossophora.

The muscular development in connexion with the whole buccal mass, and with each part of the radular apparatus, is exceedingly complicated,—as many as twenty distinct muscles having been enumerated in connexion with this organ. In addition to the radula, and correlated with its development, we find almost universally present in the Glossophora a pair of horny jaws (usually calcified) developed as cuticular productions upon the epidermis of the lips (fig. 9, A, *b*). The radula and the shelly jaws of the Glossophora enable their possessors not only to voraciously attack vegetable food, but the radula is used in some instances for boring the shells of other Mollusca, and the jaws for crushing the shells of Crustacea, and for wounding even Vertebrata.

Phylum MOLLUSCA.

Branch A.—*GLOSSOPHORA*.

Characters.—Mollusca with head-region more or less prominently developed; always provided with a peculiar rasping-tongue—the odontophore—rising from the floor of the buccal cavity.

The Glossophora comprise three classes, chiefly distinguished from one another by the modifications of the foot.

Class I.—**GASTROPODA.**

Characters.—Glossophora in which (with special exception of swimming forms) the FOOT is simple, median in position, and flattened so as to form a broad sole-like surface, by the contractions of which the animal crawls, often divided into three successive regions—the pro-, meso-, and meta-podium—by lateral constrictions.

The Gastropoda exhibit two divergent lines of descent indicated by the term sub-class (see p. 649).

Sub-class 1.—GASTROPODA ISOPLEURA.

Characters.—Gastropoda in which not only the head and foot but also the visceral dome with its contents and the mantle retain the primitive BILATERAL SYMMETRY of the archi-Mollusc. The anus retains its position in the median line at the posterior end of the body. The whole visceral mass together with the foot is elongated, so that the axis joining mouth and anus is relatively long, whilst the dorso-pedal axis at right angles to it is short. The CTENIDIA, the NEPHRIDIA, GENITAL DUCTS, and CIRCULATORY ORGANS are paired and bilaterally symmetrical. The pedal and visceral NERVE-CORDS are straight, parallel with one another, and all extend the whole length of the body; the ganglionic enlargements are feebly or not at all developed. The Isopleura comprise three orders.

Order 1.—**Polyplacophora** (the Chitons).

Characters.—Gastropoda Isopleura with a metameric repetition of the shell to the number of eight. The shells of the primitive type are partially or wholly concealed in shell-sacs comparable to the single embryonic shell-sac of other Mollusca. On the surface of the mantle-flap numerous calcified spines and knobs are frequently developed. The ctenidia are of the typical form, small in size and metamerically repeated along the sides of the body to the number of sixteen or more; an osphradium or area of "olfactory epithelium" (Spengel) is found at the base of each ctenidium. The other organs are not subject to metameric repetition. The odontophore is highly developed; the teeth of the lingual ribbon are varied in form,—several in each transverse row (fig. 9, E). Paired genital ducts distinct from the paired nephridia are present.

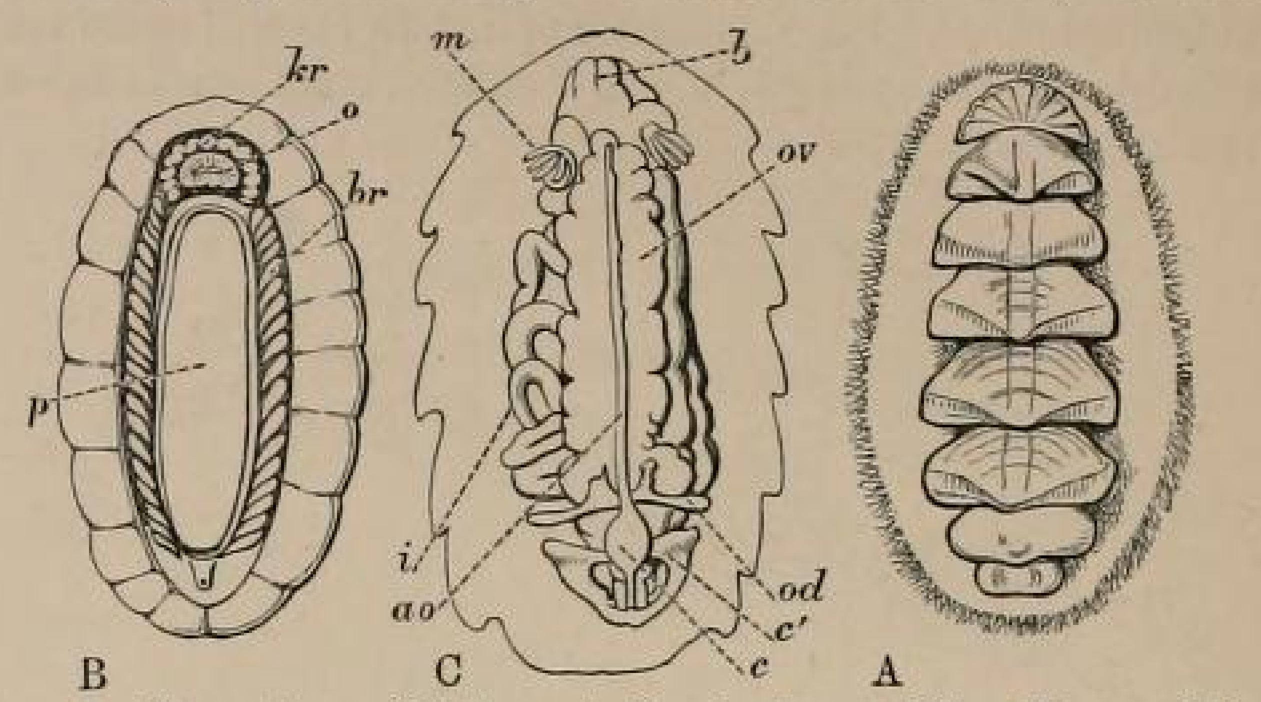


Fig. 10.—Three views of Chiton. A. Dorsal view of *Chiton Wosnessenksii*, Midd., showing the eight shells. (After Middendorf.) B. View from the pedal surface of a species of Chiton from the Indian Ocean. *p*, foot; *o*, mouth (at the other end of the foot is seen the anus raised on a papilla); *kr*, oral fringe; *br*, the numerous ctenidia (branchial plumes); spreading beyond these, and all round the animal, is the mantle-skirt. (After Cuvier.) C. The same species of Chiton, with the shells removed and the dorsal integument reflected. *b*, buccal mass; *m*, retractor muscles of the buccal mass; *ov*, ovary; *od*, oviduct; *i*, coils of intestines; *ao*, aorta; *c'*, left auricle; *c*, ventricle.

The order Polyplacophora contains but one family, the *Chitonidæ*, with the genera: *Chiton*, Lin. (figs. 10, 15, &c.); *Cryptochiton*, Midd., 1847; and *Cryptoplax* (= *Chitonellus*), Blainv., 1818.

Order 2.—**Neomeniæ.**

Characters.—Gastropoda Isopleura devoid of a shell, which is replaced by innumerable microscopic calcified plates or spicules set in the dorsal epidermis; mantle-flap not lateral, but reduced to a small collar surrounding the anus; ctenidia represented by a symmetrical group of branchial filaments on either side of the anus; foot very narrow, sunk in a groove; odontophore feebly developed, but the radula many-toothed; gonads placed in the pericardium discharging by the nephridia; no special generative ducts.

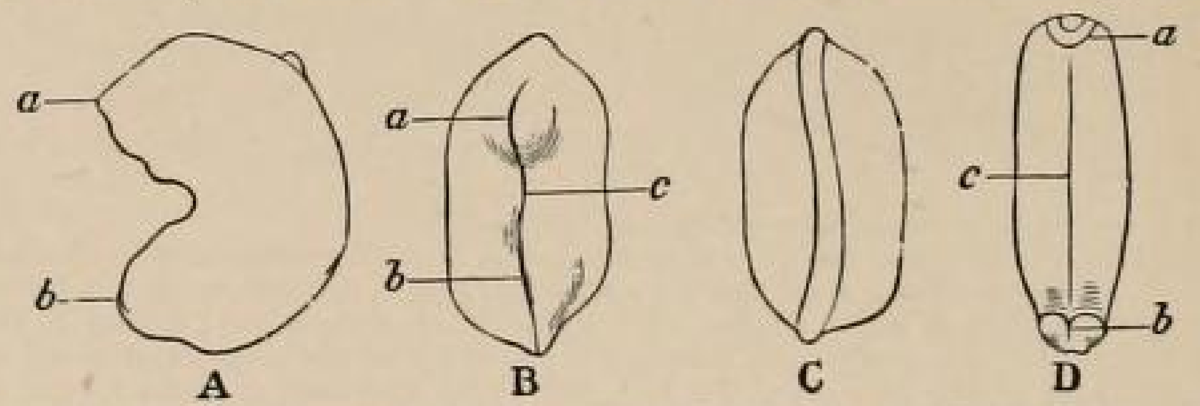


Fig. 11.—*Neomenia carinata*, Tullberg (after Tullberg). A. Lateral view. B. Ventral view. C. Dorsal view. D. Ventral view of a more extended specimen. *a*, anterior; *b*, posterior extremity; *c*, furrow, in which the narrow foot is concealed.

The order Neomeniæ contains the two genera *Neomenia*, Tullberg (*Solenopus, Sars*) (fig. 11); and *Proneomenia*, Hubrecht.

Order 3.—**Chætoderma.**

Characters.—Gastropoda Isopleura devoid of a shell, which is replaced by numerous minute calcareous spines standing up like hairs on the surface of the body; body

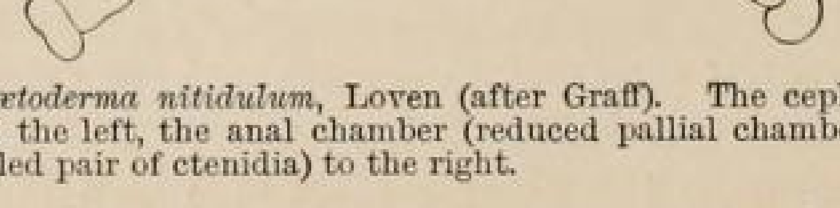


Fig. 12.—*Chætoderma nitidulum*, Loven (after Graff). The cephalic enlargement is to the left, the anal chamber (reduced pallial chamber, containing the concealed pair of ctenidia) to the right.

much elongated so as to be vermiform; mantle-flap as in Neomeniæ; ctenidia in the form of a pair of branchial plumes, one on each side of the anus; foot aborted, its position being indicated by a longitudinal furrow; odontophore greatly reduced, the radula only represented by a single tooth; gonads and nephridia as in Neomenia.

The order Chætoderma contains the single genus *Chætoderma* (fig. 12).

Further remarks on the Isopleurous Gastropods.—The union of the Chitons with the remarkable worm-like forms Neomenia and Chætoderma was rendered necessary by Hubrecht's discovery (**25**) in 1881 of a definitely constituted radula and odontophore in his new genus Proneomenia, founded on two specimens brought from the arctic regions by the Barents Dutch expedition.

By some writers—*e.g.*, Keferstein—the Chitons have been too intimately associated with the other Gastropoda, whilst, on the other hand, Gegenbaur seems to have gone a great deal too far in separating them altogether from the other Mollusca as a primary subdivision of that phylum, inasmuch as they are intimately bound to the other Glossophora by the possession of a thoroughly typical and well-developed odontophore. They undoubtedly stand nearer to the archi-Mollusca than any other Glossophora in having retained a complete bilateral symmetry and the primitive shell-sac, though the metameric repetition of this organ and of the ctenidia is a complication of, and departure from, the primitive character. It is not improbable that in the calcareous spines and plates of the dorsal integument of Neomenia and Chætoderma, which occur also on the part of the dorsum uncovered by shell in Chiton, we have the retention of a condition preceding the development of the solid Molluscan shell, or a reversion to it. The minute calcareous bodies may have the same relation to a compact shell which the shagreen denticles of the sharks have to a continuous dermal bone.

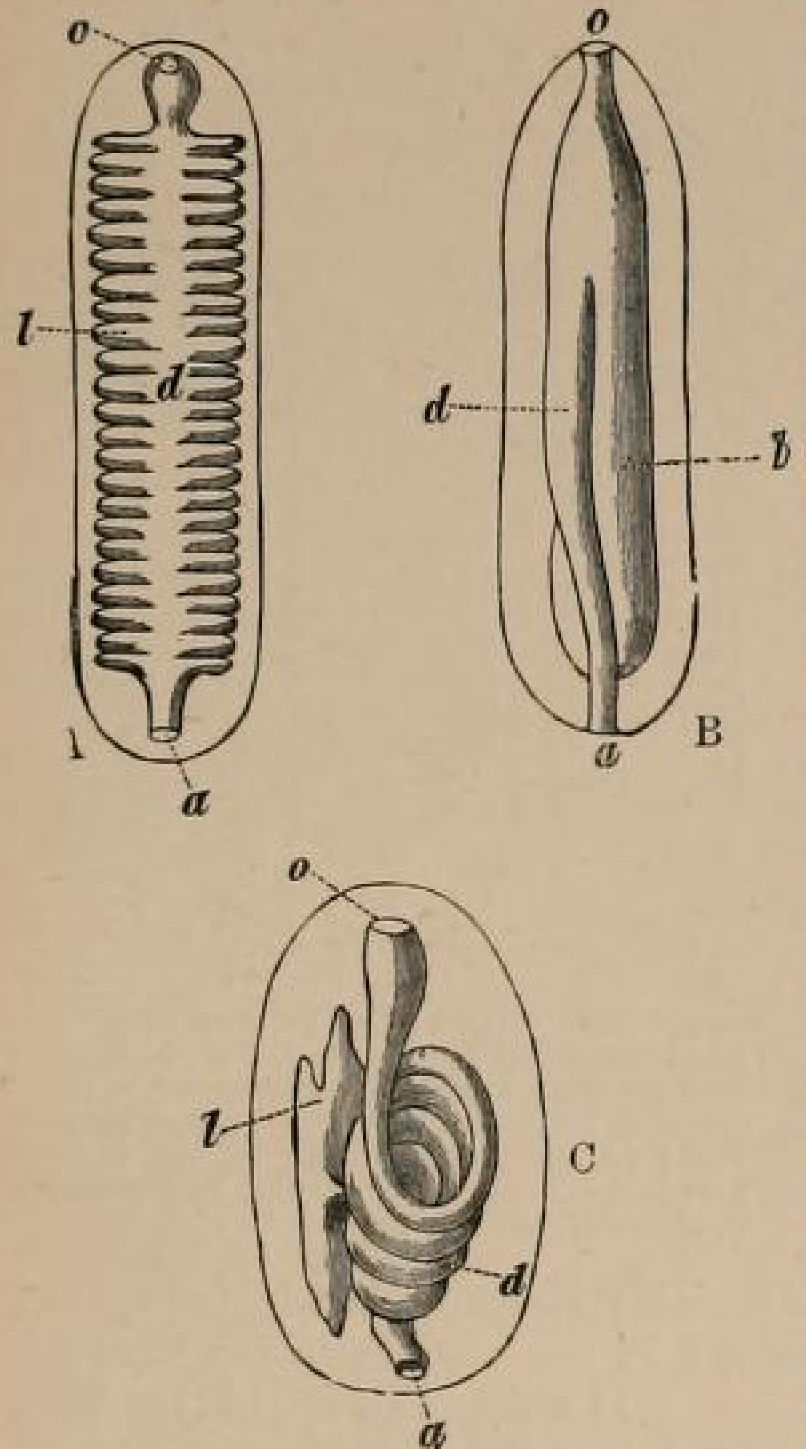


FIG. 13.—Diagrams of the alimentary canal of Isopleura (from Hubrecht). *o*, mouth; *a*, anus; *d*, alimentary canal; *l*, liver (digestive gland). A. Neomenia and Proneomenia. B. Chætoderma. C. Chiton.

The anatomy of the Gastropoda Isopleura has been largely elucidated within the past year by the researches of Hubrecht and of Sedgwick, who have been the first to apply the method of sections to the study of this group.

The leading points in the modifications of mantle-flap, foot, and ctenidia are set forth in the preceding summaries, and in the accompanying references to the figures. With regard to other organs, we have to note the form of the alimentary canal (fig. 13), which is simplest in Chætoderma, symmetrically sacculated in Neomenia, and wound upon itself, forming a few coils, in Chiton. The latter has a compact liver with arborescent duct, which is represented by the sacculi in Neomenia and by a single cæcum in Chætoderma. Salivary glands are present in Chiton and in Proneomenia. The radula is highly developed in Chiton, and, though present in Proneomenia, has not been described in Neomenia. A single tooth in Chætoderma appears to represent the radula in a reduced state. The circulatory organs of Chiton alone are known with any degree of detail (fig. 10, C). There is a median dorsal blood-vessel—the aorta—which is enlarged to form a ventricle in the posterior region of the body. On either side the ventricle is connected to a well-developed auricle, which pours into it the aerated blood from the gills (ctenidia). The extent to which vascular trunks are developed has not been determined, but vessels to and from the ctenidia, and in the mid-line of the foot, are known. As in other Mollusca, the vessels do not extend far, but lead into lacunæ between the organs and tissues. Dorsal and ventral vessels have been detected in Neomenia and Chætoderma, but no specialized heart.

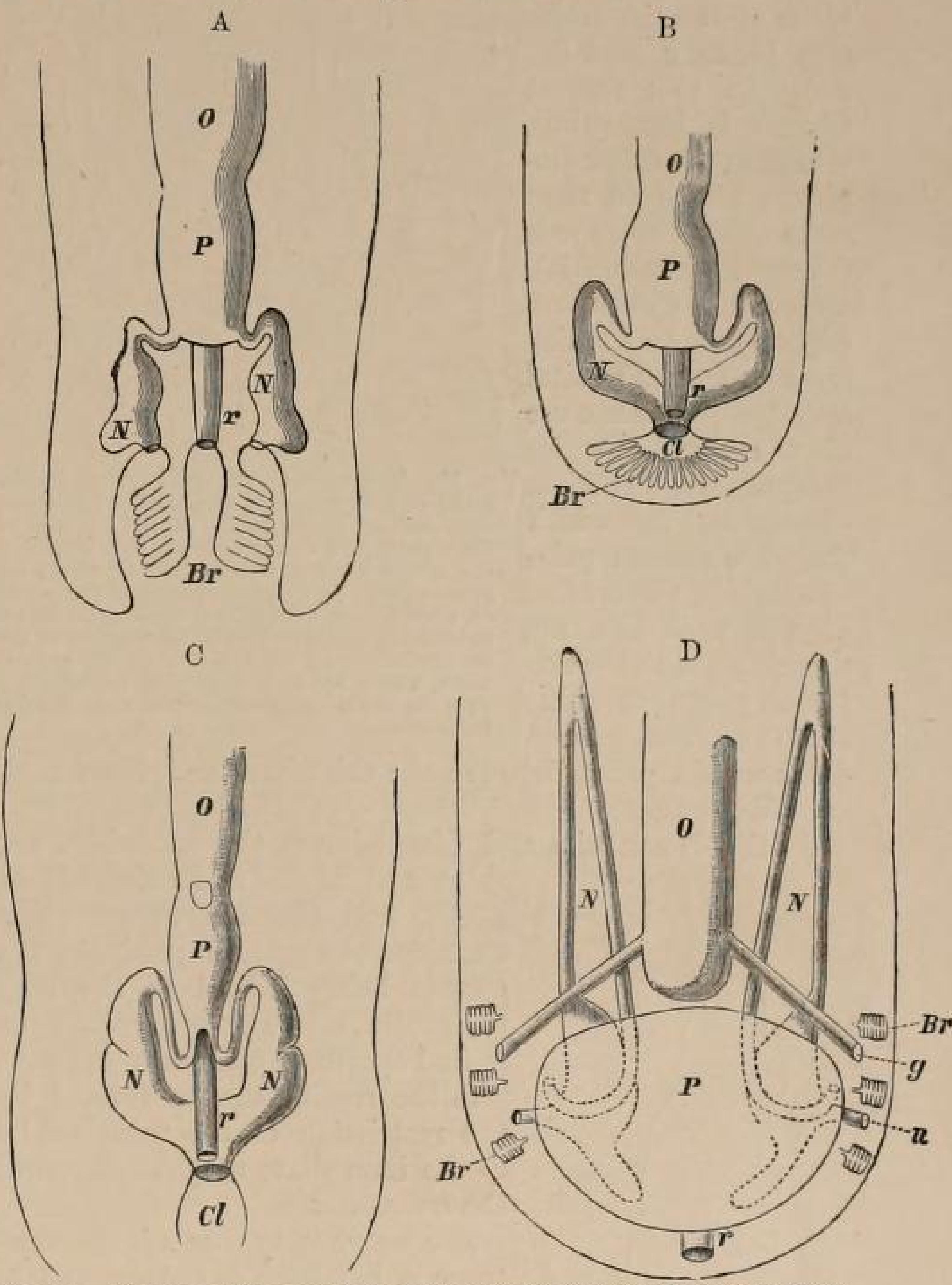


FIG. 14.—Diagrams of the excretory and reproductive organs of Isopleura (after Hubrecht). *O*, ovary; *P*, pericardium; *N*, nephridium; *u*, external aperture of nephridium; *g*, external aperture of the genital duct of Chiton; *r*, rectum; *Cl*, cloacal or pallial chamber of Neomeniæ and Chætoderma; *Br*, ctenidia (branchial plumes). A. Chætoderma. B. Neomenia. C. Proneomenia. D. Chiton.

The heart of Chiton lies in a space which is to be regarded as a specialized part of the cœlom, and, as in other Molluscs, is termed the pericardium. In front of this space in Chiton lies the ovary (fig. 14, D). In the other Isopleura the genital bodies (gonads) lie in the pericardium, which has a longer form and extends dorsally above the intestine. Opening into the pericardium equally in all the Isopleura (fig. 14) is a pair of bent tubes which lead to the exterior. These are the nephridia, which in Chiton are essentially renal in function. Their disposition has been determined by Sedgwick (**26**), who has shown that each nephridium is much bent on itself, so that, as in the nephridia of Conchifera (organ of Bojanus), the internal aperture lies near the external. From the folded stem of the nephridium very numerous secreting cæca are given off, —omitted in the diagram (fig. 14, D), but accurately drawn in fig. 15. The sexes in Chiton are distinct, and the ovary or testis, as the case may be, though lying in and filling a chamber of the original cœlom, does not discharge into the pericardium, but has its own ducts, which pass to the exterior just in front of those of the nephridia (fig. 14, D, *g*, and fig. 16). In this respect Chiton is less primitive than the other Isopleura, and even than some other Gastropods (the Zygobranchia), and some Conchifera (Spondylus, &c.), which have no special genital apertures, but make use of the nephridia for this purpose. In *Chiton discrepans*, in which there are sixteen pairs of ctenidia, the orifices of the nephridia are coincident with the sixteenth pair of ctenidia, those of the genital ducts with a point between the thirteenth and fourteenth ctenidia.

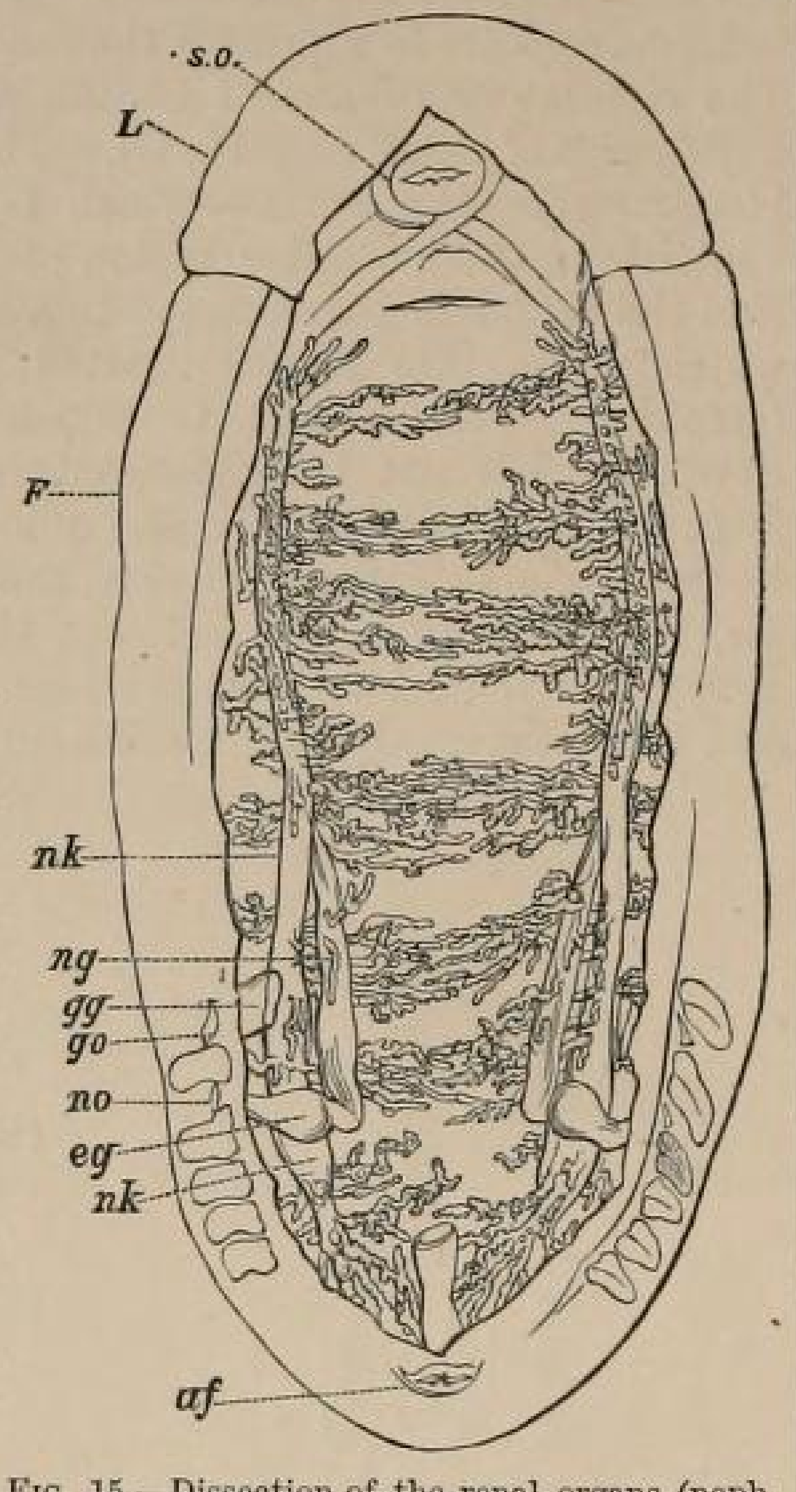


Fig. 15.—Dissection of the renal organs (nephridia) of *Chiton siculus*, after Haller (*Arbeiten, Zool. Instit.*, Vienna, 1882). *F*, foot; *L*, edge of the mantle not removed in the front part of the specimen; *s.o.*, œsophagus; *af*, anus; *gg*, genital duct; *go*, external opening of the same; *eg*, stem of the nephridium leading to *no*, its external aperture; *nk*, reflected portion of the nephridial stem; *ng*, fine cæca of the nephridium, which are seen ramifying transversely over the whole inner surface of the pedal muscular mass.

In the Neomeniæ and Chætoderma the nephridia are short and wide (*N* in fig. 14, A, B, C), and function as excretory ducts for the genital products, the gonads being lodged in the long pericardium. Their separate or united apertures open near the anus into the small chamber formed by the restriction of the mantle-skirt to the immediate neighbourhood of the anus.

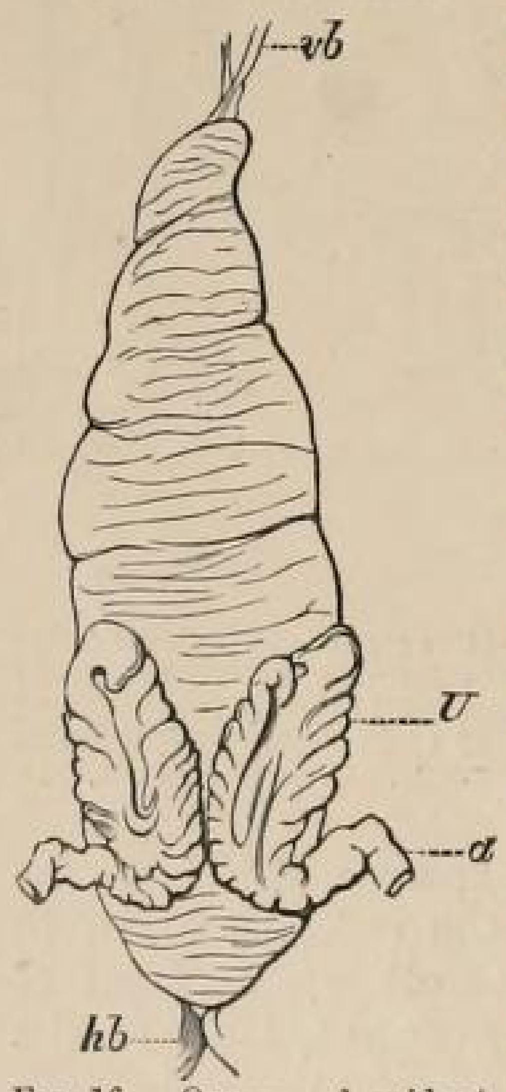


Fig. 16.—Ovary and oviducts of *Chiton siculus* (after Haller, *loc. cit.*). *vb*, *hb*, anterior and posterior suspensor of the ovary; *U*, uterus (enlarged part of oviduct); *a*, oviduct.

The nervous system of the Gastropoda Isopleura is represented in the diagram fig. 17. In all it is important to observe that nerve-ganglion cells are by no means limited to special swellings—the ganglia—but are abundant along the whole course of the four great longitudinal trunks. This is a primitive character comparable to that presented by the nerve-cords of Nemertine worms, and of the Arthropod Peripatus. Higher differentiation in other Mollusca leads to predominance if not an exclusive presence of nerve-*fibres* in the cords, and of nerve-*ganglion cells* in the specialized ganglia. The numerous transverse connexions of the pedal nerve-cords in Chiton and Neomenia (seen also in Fissurella (fig. 36) and some other Gastropods) are comparable to the transverse connexions of the ventral nerve-cords of Chætopod worms and Arthropods. In the abundance of the nervous network connected with its longitudinal nerve-tracts, Chiton appears to retain something of the early condition of the Cœlomate nervous system when it had the form of a sub-epidermic network or nerve-tunic (seen more clearly in Planarians and some Nemertines), and when the concentration into definitely compacted cords had not set in.

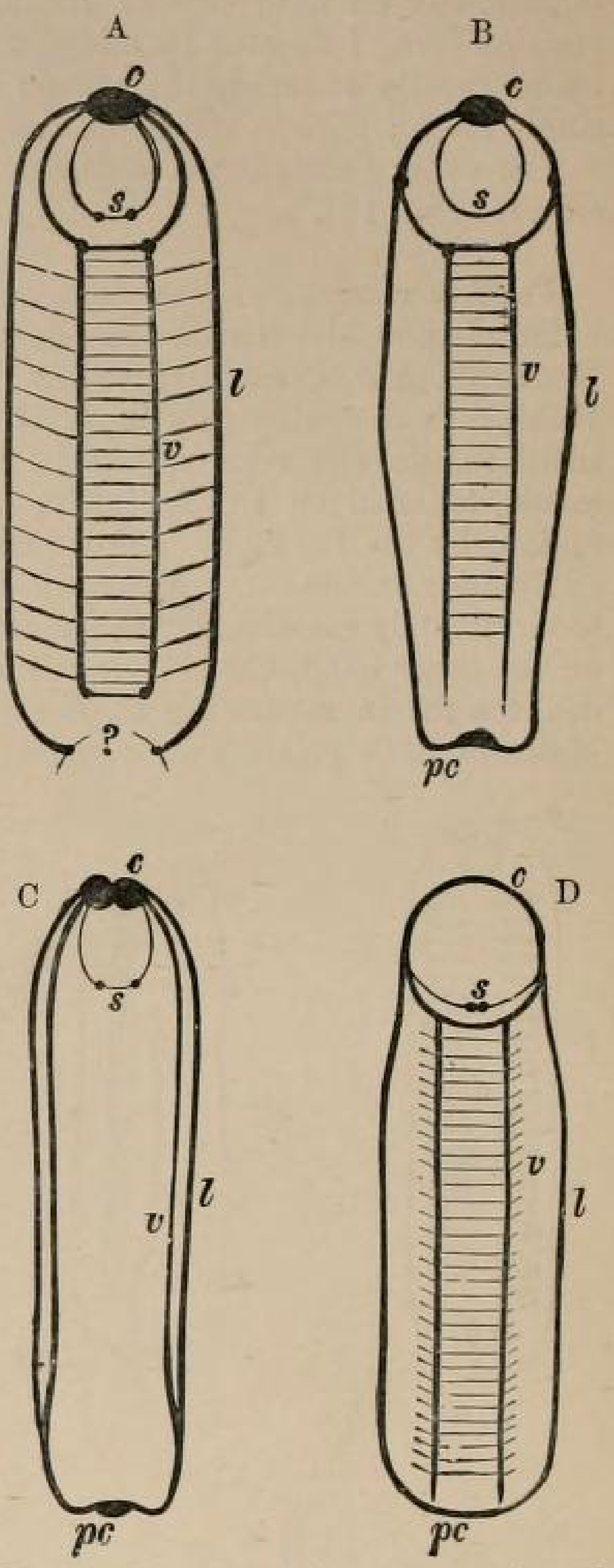


Fig. 17.—Diagrams of the nervous system of Isopleura (after Hubrecht, *loc. cit.*). *c*, cerebral ganglia; *s*, sublingual ganglia; *v*, pedal (ventral) nerve-cord; *l*, visceral (lateral) nerve-cord; *pc*, post-anal junction of the visceral nerve-cords. A. Proneomenia. B. Neomenia. C. Chætoderma. D. Chiton.

Ganglia are, however, distinguishable upon the nervous cords of Chiton (fig. 18). The cerebral ganglia are not distinguishable as such, but a pair of buccal ganglia (B in fig. 18) are developed on two connectives which pass forward from the cerebral region to the great muscular mass of the mouth. These buccal ganglia are special developments connected with the special muscularity of the lips and odontophore, and are found in all Glossophora, but not in the Lipocephala. Such special ganglia related to special organs (and not introduced in our schematic Mollusc, fig. 1) we find in connexion with the siphons of the Lipocephala, and in various positions upon the visceral nerve-cords of other Mollusca, both Glossophora and Lipocephala. A pair of pedal ganglia but little developed (*p* in fig. 18), and a special group of sublingual gãnglia are present in Chiton. On the whole, the nervous system of the Isopleura is exceedingly simple and archaic, whilst it does not well serve as a type with which to compare that of other Mollusca on account of the small amount of concentration of its nerve-ganglion cells into ganglia, such as we find well developed in other forms.

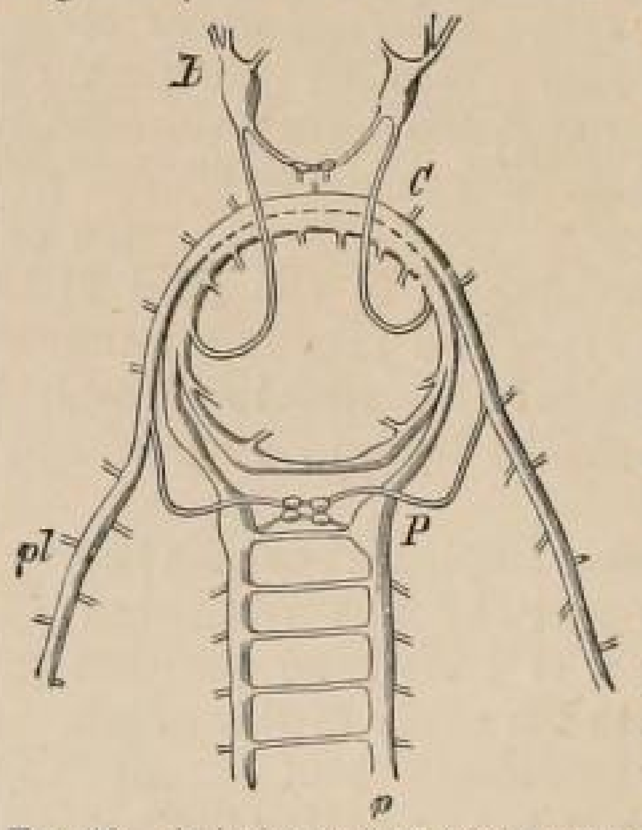


Fig. 18.—Anterior part of the nervous system of *Chiton cinereus*, in more detail (from Gegenbaur, *Elements of Comp. Anatomy*). *B*, buccal ganglia (concerned with the odontophore); *C*, cerebral nerve-mass; *P*, pedal ganglion and commencement of pedal nerve-cord; *pl*, visceral nerve-cord. The sublingual ganglia are not lettered.

The development of Neomenia and Chætoderma from the egg is entirely unknown, that of Chiton only partially. Impregnation is effected when the eggs have been discharged and are lying beneath the mantle-skirt. A trochosphere larva is developed from the Diblastula of Chiton (Loven).

The Chitons are found in the littoral zone in all parts of the world, and are exclusively marine. Neomenia, Proneomenia, and Chætoderma have hitherto been dredged from considerable depths (100 fathoms and upwards) in the North Sea, Proneomenia also in the Mediterranean (Marion).

Sub-class 2.—GASTROPODA ANISOPLEURA.

Characters.—Gastropoda in which, whilst the head and foot retain the bilateral symmetry of the archi-Mollusca, the visceral dome, including the mantle-flap dependent from it, and the region on which are placed the ctenidia, anus, generative and nephridial apertures, have been subjected to a ROTATION tending to bring the anus from its posterior median position, by a movement along the right side, forwards to a position above the right side of the animal's neck, or even to the middle line above the neck. This torsion is connected mechanically with the excessive vertical growth of the visceral hump and the development upon its surface of a heavy shell. The SHELL is not a plate enclosed in a shell-sac, but the primitive shell-sac appears and disappears in the course of embryonic development, and a relatively large nautiloid shell (with rare exceptions) develops over the whole surface of the visceral hump and mantle-skirt. Whilst such a shell might retain its median position in a swimming animal, it and the visceral hump necessarily fall to one side in a creeping animal which carries them uppermost.

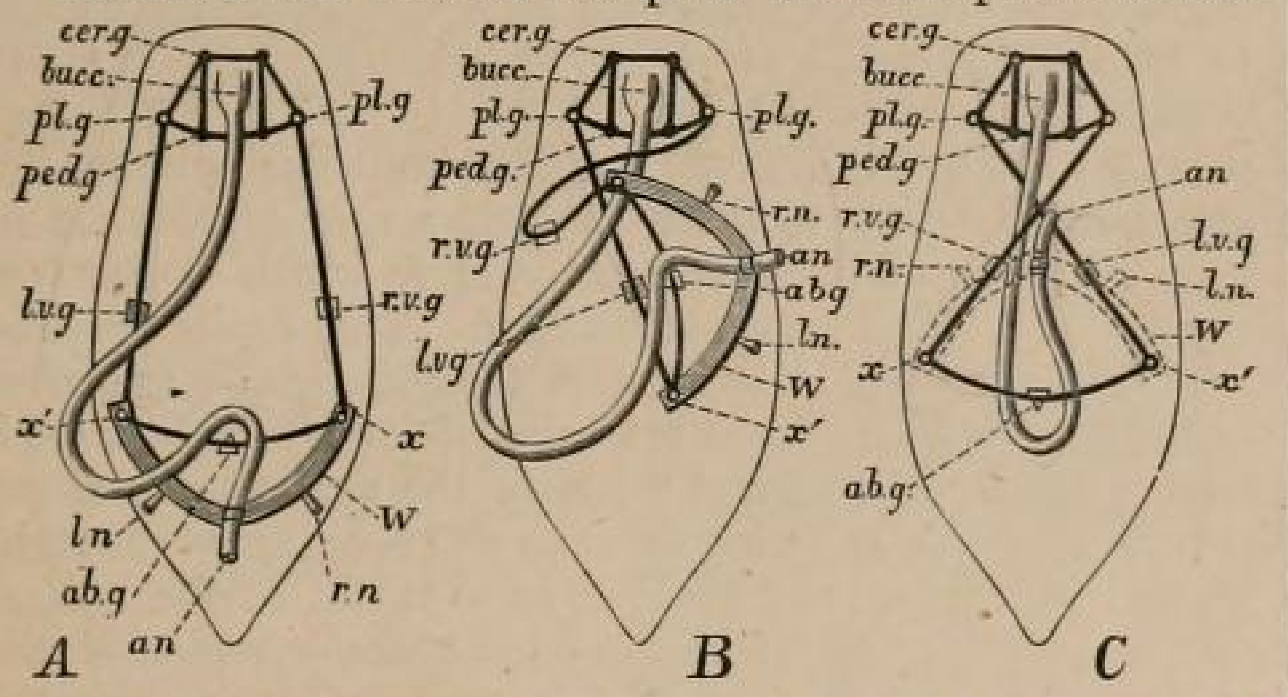


FIG. 19.—Sketch of a model designed so as to show the effect of torsion or rotation of the visceral hump in Streptoneurous Gastropoda; *A*, unrotated ancestral condition, *B*, quarter-rotation; *C*, complete semi-rotation (the limit); *an*, anus; *ln*, *rn*, primarily left nephridium and primarily right nephridium; *lvg*, primarily left (subsequently the sub-intestinal) visceral ganglion; *rvg*, primarily right (subsequently the sub-intestinal) visceral ganglion; *cerg*, cerebral ganglion; *plg*, pleural ganglion; *pedg*, pedal ganglion; *abg*, abdominal ganglion; *bucc*, buccal mass; *W*, wooden arc representing the base-line of the wall of the visceral hump; *x*, *x'*, pins fastening the elastic cord (representing the visceral nerve loop) to *W*.

The shell and visceral hump in the Anisopleura incline normally to the right side of the animal. As mechanical results, there arise a one-sided pressure and a one-sided strain, together with a one-sided development of the muscular masses which are related to the shell and foot. Both the TORSION THROUGH A SEMICIRCLE of the base of the visceral dome and the continued leiotropic spiral growth of the visceral dome itself, which is very usual in the Anisopleura, appear to be traceable to these mechanical conditions. ATROPHY of the representatives on one side of the body of paired organs is very usual. Those placed primitively on the left side of the rectum, which in virtue of the torsion becomes the right side, are the set which suffer (see fig. 19). Some Anisopleura, after having thus acquired a strongly-marked inequilateral character in regard to such organs as the ctenidia, nephridia, genital ducts, heart, and rectum, appear by further change of conditions of growth to have acquired a superficial bilateral symmetry, the secondary nature of which is revealed by anatomical examination (Opisthobranchia, Natantia).

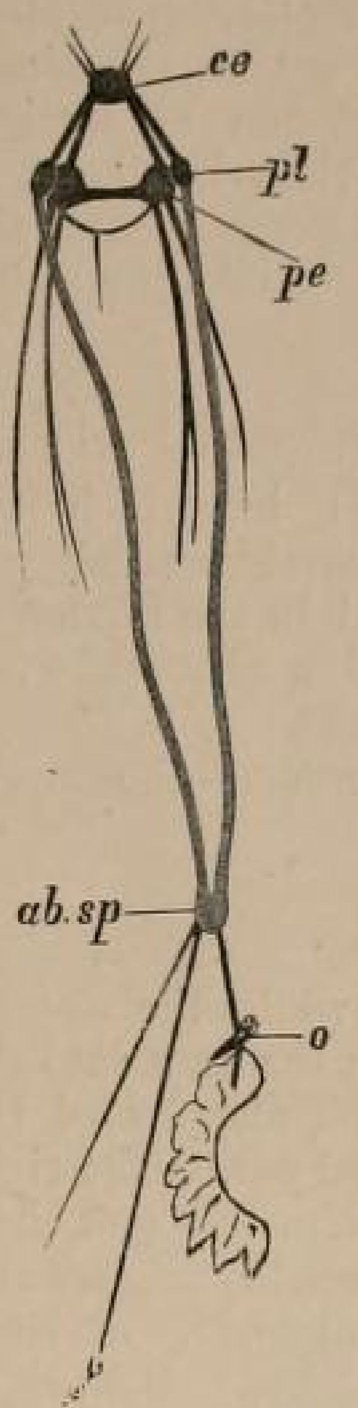


FIG. 20.—Nervous system of Aplysia, as a type of the long-looped Euthyneurous condition. The untwisted visceral loop is lightly shaded. *ce*, cerebral ganglion; *pl*, pleural ganglion; *pe*, pedal ganglion; *ab. sp*, abdominal ganglion, which represents also the supra-intestinal ganglion of Streptoneura and gives off the nerve to the osphradium (olfactory organ) *o*, and another to an unlettered so-called "genital" ganglion. The buccal nerves and ganglia are omitted. (After Spengel.)

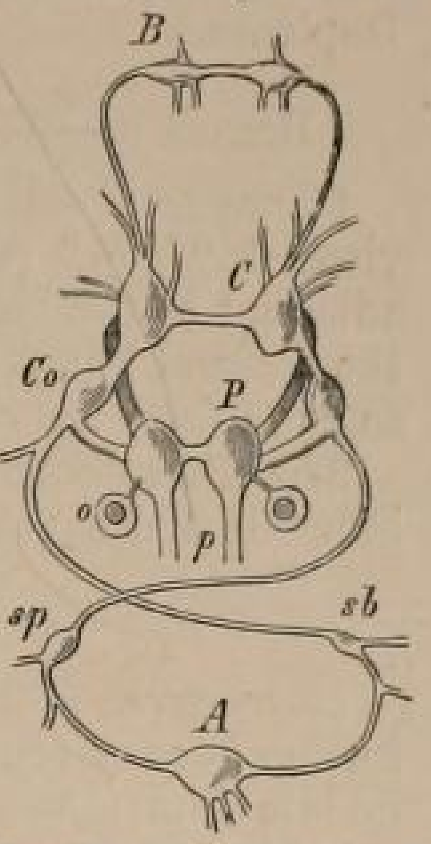


FIG. 21.—Nervous system of Paludina as a type of the Streptoneurous condition. *B*, buccal (sub-œsophageal) ganglion; *C*, cerebral ganglion; *Co*, pleural ganglion; *P*, pedal ganglion with otocyst attached; *p*, pedal nerve; *A*, abdominal ganglion at the extremity of the twisted visceral "loop"; *sp*, supra-intestinal visceral ganglion on the course of the right visceral cord; *sb*, sub-intestinal ganglion on the course of the left visceral cord. (From Gegenbaur, after Jhering.)

In all groups of Anisopleura examples are numerous in which the shell is greatly developed, forming a "house" into which the whole animal can be withdrawn, the entrance being often closed by a second shelly piece carried upon the foot (the operculum). The power of rapidly extending and of again contracting large regions of the body to an enormous degree is usual, as in the Lipocephalous Mollusca. In spite of the theories which have been held on this matter, it appears highly probable that no fluid from without is introduced into the blood, nor is any expelled during these changes of form. A large mucous gland with a median pore is usually developed on the ventral surface of the foot, comparable to the similar gland and pore in Lipocephala, and in some cases (*e.g.*, Pyrula, fig. 37, B) this has been mistaken for a water-pore.

The leiotropic torsion of the visceral dome has had less deep-seated effect in one series of Anisopleura than in another. Accordingly, as the loop formed by the two VISCERAL NERVES (fig. 19) is or is not caught, as it were, in the twist, we are able to distinguish one branch or line of descent with straight visceral nerves—the EUTHYNEURA (fig. 20)—from a second branch with the visceral nerves

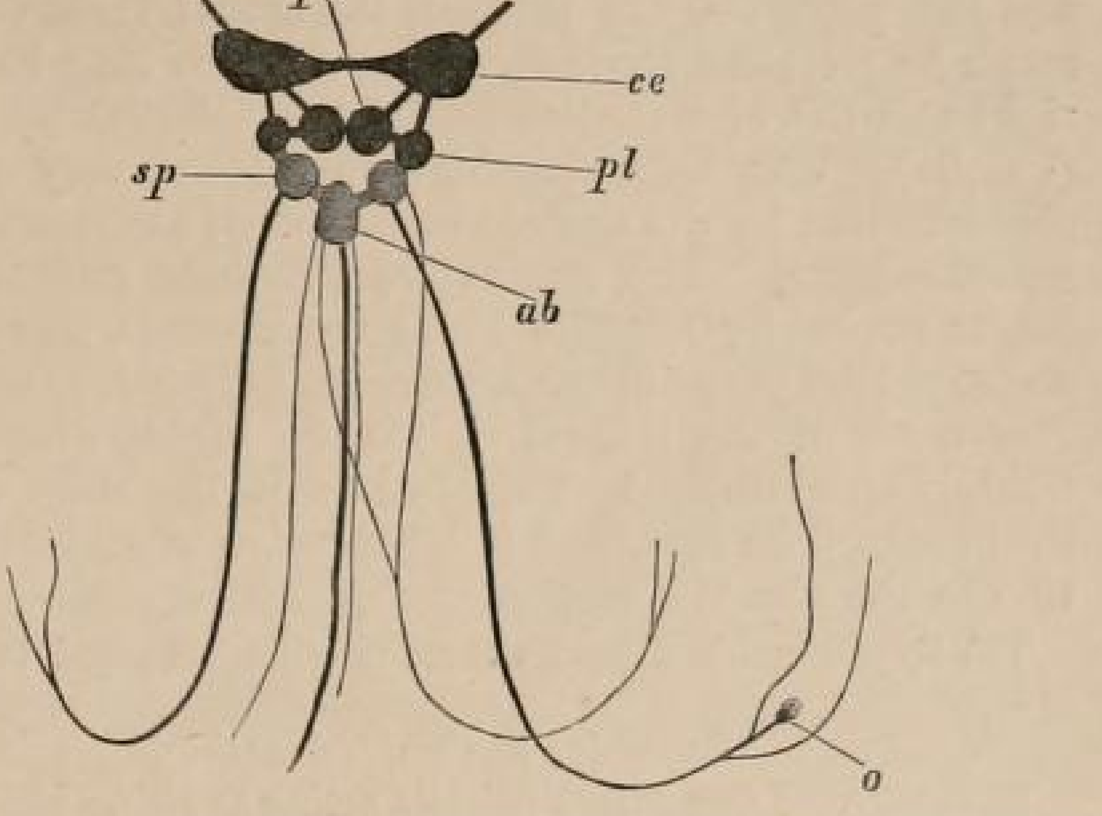


FIG. 22.—Nervous system of the Pond-Snail, *Limnæus stagnalis*, as a type of the short-looped Euthyneurous condition. The short visceral "loop" with its three ganglia is lightly-shaded. *ce*, cerebral ganglion; *pe*, pedal ganglion; *pl*, pleural ganglion; *ab*, abdominal ganglion; *sp*, visceral ganglion of the left side; opposite to it is the visceral ganglion of the right side, which gives off the long nerve to the olfactory ganglion and osphradium *o*. In Planorbis and in Auricula (Pulmonata, allied to Limnæus) the olfactory organ is on the *left* side and receives its nerve from the *left* visceral ganglion. (After Spengel.)

twisted into a figure-of-eight—the **Streptoneura** (fig. 21). Probably the Euthyneura and the Streptoneura have developed independently from the ancestral bilaterally symmetrical Gastropods. The escape of the visceral nerve-loop from the torsion depends on its having acquired a somewhat deeper position and shorter extent, previously to the commencement of the phenomenon of torsion, in the ancestors of the Euthyneura than in those of the Streptoneura. In the ancestral Streptoneura the visceral loop was lateral and superficial as in the living Isopleura.

Branch *a.—STREPTONEURA* (Spengel, 1881).

Characters.—Gastropoda Anisopleura in which the visceral "loop" (the conterminous visceral nerves) was adherent to the body-wall and so shared in the torsion of the visceral hump, the right cord crossing above the left so as to form a figure-of-eight (see fig. 19).

The Streptoneura comprise two orders—the Zygobranchia and the Azygobranchia.

Order 1.—**Zygobranchia.**

Characters.—Streptoneura in which, whilst the visceral torsion is very complete so as to bring the anus into the middle line anteriorly or nearly so, the atrophy of the primitively left-side organs is not carried out. The right and left ctenidia, which have now become left and right respectively, are of equal size, and are placed symmetrically on either side of the neck in the pallial space. Related to them is a simple pair of osphradial patches. Both right and left nephridia are present, the actual right one being much larger than the left. Two auricles may be present right and left of a median ventricle (Haliotis), or only one (Patella). The Zygobranchia are further very definitely characterized by the archaic character of absence of special genital ducts. The generative products escape by the larger nephridium. The sexes are distinct, and there is no copulatory or other accessory generative apparatus. The teeth of the lingual ribbon are highly differentiated (Rhipidoglossate). The visceral dome lies close upon the oval sucker-like foot, and is coextensive with its prolongation in the aboral direction.

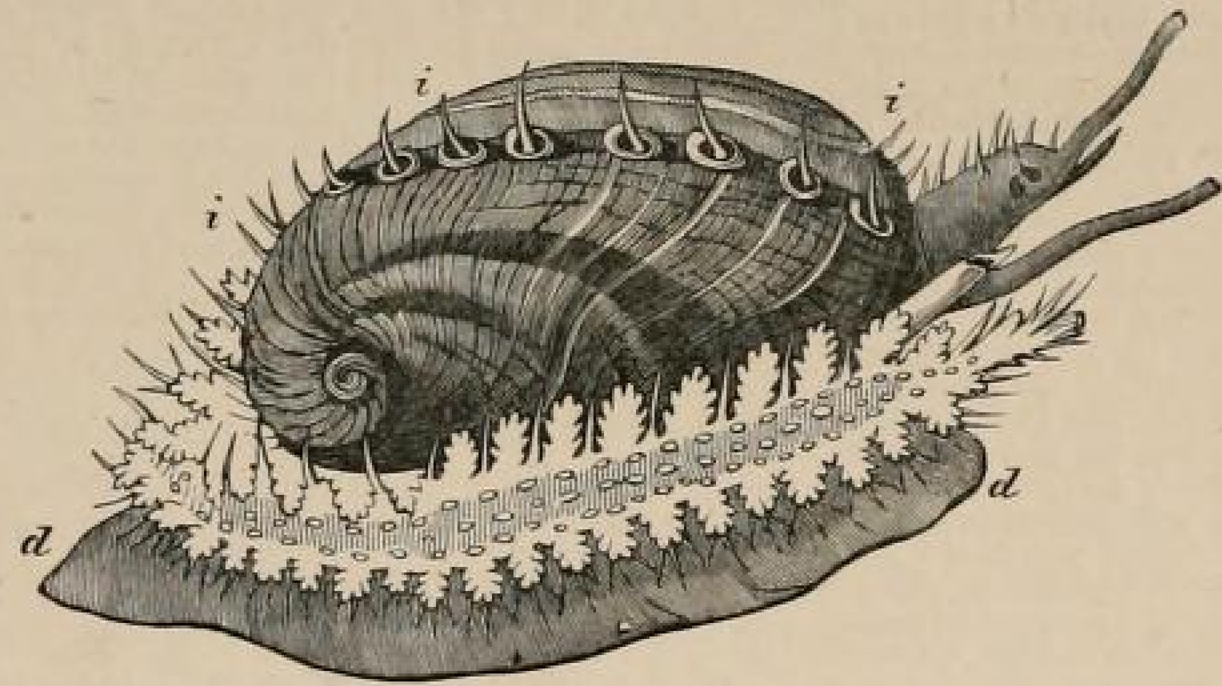


Fig. 23.—*Haliotis tuberculata.* *d*, foot; *i*, tentacular processes of the mantle. (From Owen, after Cuvier.)

The Zygobranchia comprise three families, arranged in two sub-orders.

Sub-order 1. *Ctenidiobranchia.*

Character.—Large paired ctenidia acting as gills.

Family 1.—*Haliotidæ.*

Genera: *Haliotis* (Ear-Shell, Ormer in Guernsey); mostly tropical; *Teinotis.*

Family 2.—*Fissurellidæ.*

Genera: *Fissurella* (Key-hole Limpet) (figs. 24, 36), *Emarginula*, *Parmophorus* (fig. 25); mostly tropical.

Sub-order 2. *Phyllidiobranchia.*

Characters.—Ctenidia reduced to wart-like papillæ; special sub-pallial lamellæ, similar to those of the Opisthobranch Pleurophyllidia, perform the function of gills.

Family 3.—*Patellidæ.*

Genera: *Patella* (Limpet, figs. 26, &c.), *Nacella* (Bonnet-Limpet), *Lottia.*

Further Remarks on Zygobranchia.—The Common Limpet is a specially interesting and abundant example of the remarkable order Zygobranchia. A complete and accurate account of its anatomy has yet to be written. Here we have only space for a brief outline. The foot of the Limpet is a nearly circular disc of muscular tissue; in front, projecting from and raised above it, are the head and neck (figs. 26, 30). The visceral hump forms a low conical dome above the sub-circular foot, and standing out all round the base of this dome so as to completely overlap the head and foot, is the circular mantle-skirt. The depth of free mantle-skirt is greatest in front, where the head and neck are covered in by it. Upon the surface of the visceral dome, and extending to the edge of the free mantle-skirt, is the conical shell. When the shell is taken away (best effected by immersion in hot water) the surface of the visceral dome is found to be covered by a black-coloured epithelium, which may be removed, enabling the observer to note the position of some organs lying below the transparent integument (fig. 27). The muscular columns (*c*) attaching the foot to the shell form a ring incomplete in front, external to which is the free mantle-skirt. The limits of the large area formed by the flap over the head and neck (*ecr*) can be traced, and we note the anal papilla showing through and opening on the right shoulder, so to speak, of the animal into the large anterior region of the sub-pallial space. Close to this the small renal organ (*i*, mediad) and the larger renal organ (*k*, to the right and posteriorly) are seen, also the pericardium (*l*) and a coil of the intestine (*int*) embedded in the compact liver.

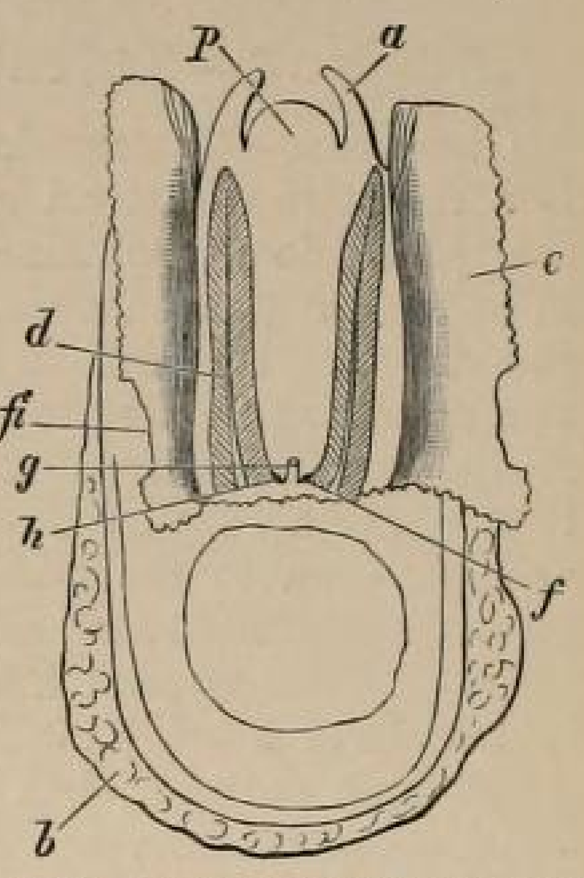


Fig. 24.—Dorsal aspect of a specimen of Fissurella from which the shell has been removed, whilst the anterior area of the mantle-skirt has been longitudinally slit and its sides reflected. *a*, cephalic tentacle; *b*, foot; *d*, left (archaic right) gill-plume; *e*, reflected mantle-flap; *fi*, the fissure or hole in the mantle-flap traversed by the longitudinal incision; *f*, right (archaic left) nephridium's aperture; *g*, anus; *h*, left (archaic right) aperture of nephridium; *p*, snout. (Original.)

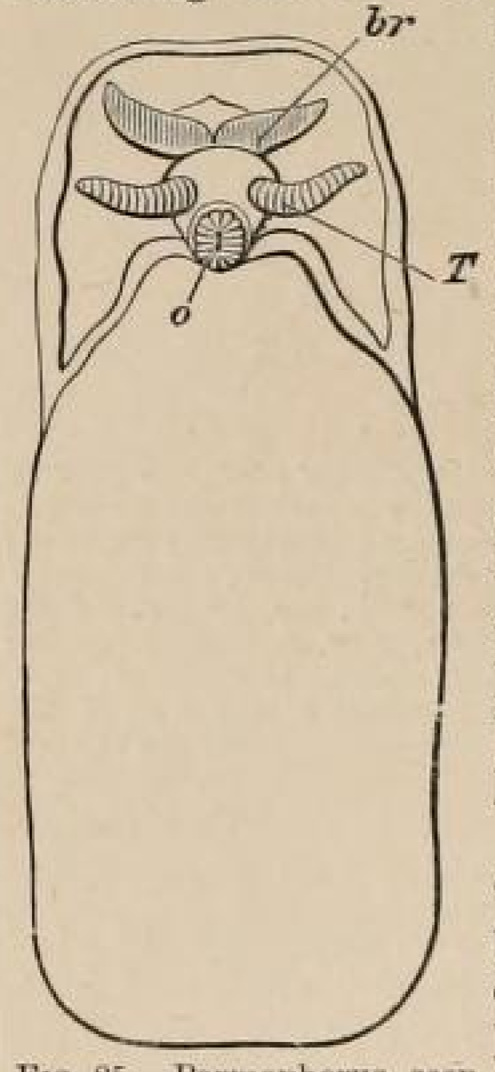


Fig. 25.—Parmophorus, seen from the pedal surface. *o*, mouth; *T*, cephalic tentacle; *br*, one of the two symmetrical gills placed on the neck. (Original.)

On cutting away the anterior part of the mantle-skirt so as to expose the sub-pallial chamber in the region of the neck, we find the right and left renal papillæ (discovered by Lankester (**27**) in 1867) on either side the anal papilla (fig. 28), but no gills. If a similar examination be made of the allied genus Fissurella (fig. 24, *d*), we find right and left of the two renal apertures a right and left gill-plume or ctenidium, which by their presence here and in Haliotis furnish the distinctive character to which the name Zygobranchia refers. In Patella no such plumes exist, but right and left of the neck are seen a pair of minute oblong yellow bodies (fig. 28, *d*), which were originally described by Lankester as orifices possibly connected with the evacuation of the generative products. On account of their position they were termed by him the "capito-pedal orifices," being placed near the junction of head and foot. Spengel (**24**) has, however, in a most ingenious way shown that these bodies are the representatives of the typical pair of ctenidia, here reduced to a mere rudiment. Near to each rudimentary ctenidium Spengel has discovered an olfactory patch or osphradium (consisting of modified epithelium) and an olfactory nerve-ganglion (fig. 32). It will be remembered that, according to Spengel, the osphradium of Mollusca is definitely and intimately related to the gill-plume or ctenidium, being always placed near the base of that organ; further, Spengel has shown that the nerve-supply of this olfactory organ is always derived from the visceral loop. Accordingly, the nerve-supply affords a means of testing the conclusion that we have in Lankester's capito-pedal bodies the rudimentary ctenidia. The accompanying diagrams (figs. 34, 35) of the nervous systems of Patella and of Haliotis, as determined by Spengel, show the identity in the origin of the nerves passing from the visceral loop to Spengel's olfactory ganglion of the Limpet, and that of the nerves which pass from the visceral loop of Haliotis to the olfactory patch or osphradium, which lies in immediate relation on the right and on the left side to the right and the left gill-plumes (ctenidia) respectively. The same diagrams serve to demonstrate the Streptoneurous condition of the visceral loop in Zygobranchia.

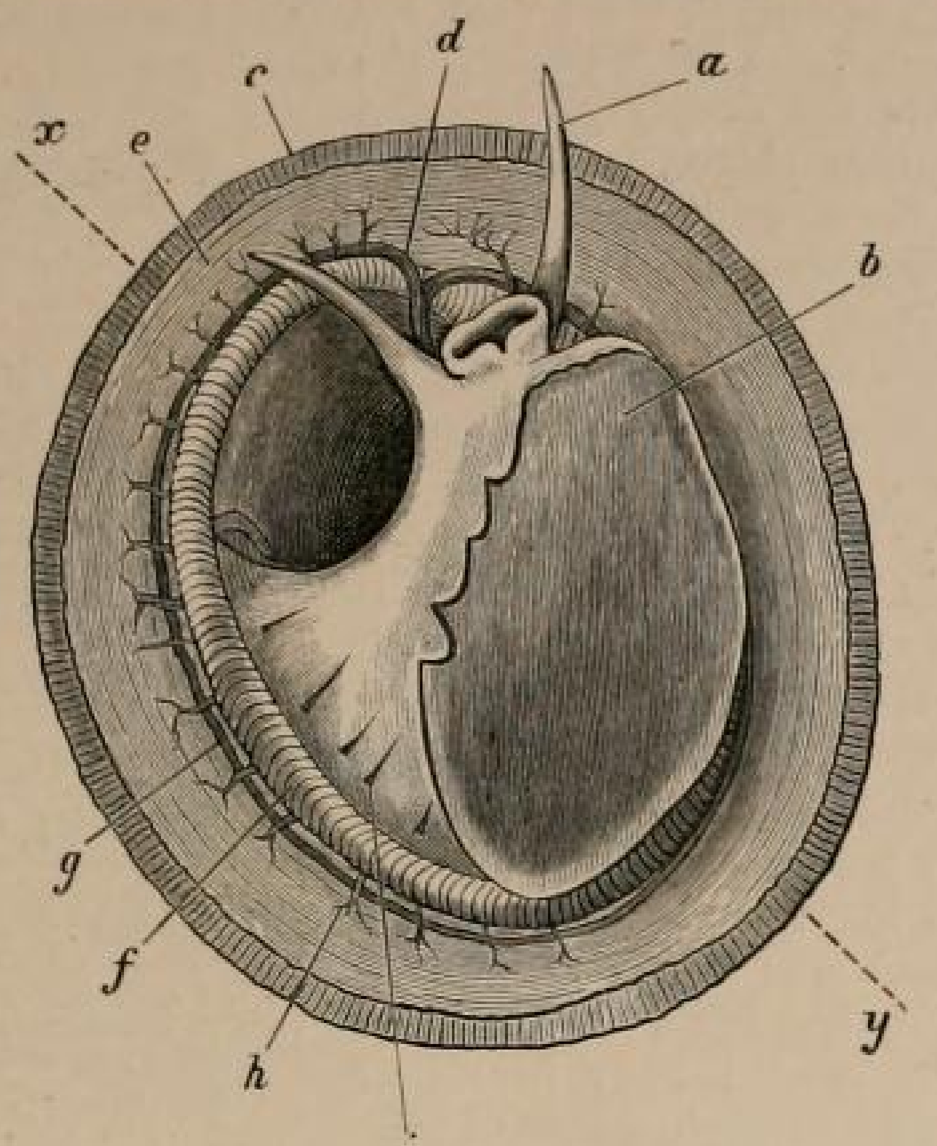


Fig. 26.—The Common Limpet (*Patella vulgata*) in its shell, seen from the pedal surface. *x*, *y*, the median antero-posterior axis; *a*, cephalic tentacle; *b*, plantar surface of the foot; *c*, free edge of the shell; *d*, the branchial efferent vessel carrying aerated blood to the auricle, and here interrupting the circlet of gill lamellæ; *e*, margin of the mantle-skirt; *f*, gill lamellæ (*not* ctenidia, but special pallial growths, comparable to those of Pleurophyllidia); *g*, the branchial efferent vessel; *h*, factor of the branchial advehent vessel; *i*, interspaces between the muscular bundles of the root of the foot, causing the separate areæ seen in fig. 27, *c*. (Original.)

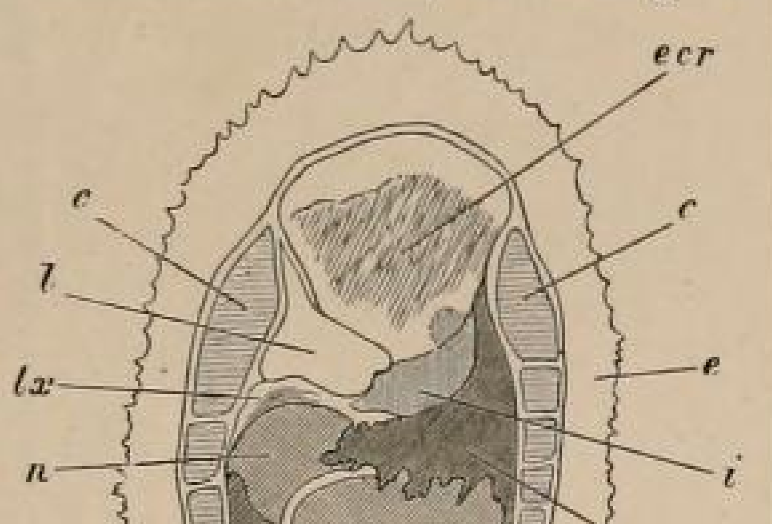


Fig. 27.—Dorsal surface of the Limpet removed from its shell and deprived of its black pigmented epithelium; the internal organs are seen through the transparent body-wall. *c*, muscular bundles forming the root of the foot, and adherent to the shell; *e*, free mantle-skirt; *em*, tentaculiferous margin of the same; *i*, smaller (left) nephridium; *k*, larger (right) nephridium; *l*, pericardium; *lx*, fibrous septum, behind the pericardium; *n*, liver; *int*, intestine; *ecr*, anterior area of the mantle-skirt overhanging the head (cephalic hood). (Original.)

Thus, then, we find that the Limpet possesses a symmetrically-disposed pair of ctenidia in a rudimentary condition, and justifies its position among Zygobranchia. At the same time it possesses a totally distinct series of *functional* gills, which are not derived from the modification of the typical Molluscan ctenidium. These gills are in the form of delicate lamellæ (fig. 26, *f*), which form a series extending completely round the inner face of the depending mantle-skirt. This circlet of gill-lamellæ led Cuvier to class the Limpets as Cyclobranchiata, and, by erroneous identification of them with the series of metamerically repeated ctenidia of Chiton, to associate the latter Mollusc with the former. The gill-lamellæ of Patella are processes of the mantle comparable to the plait-like folds often observed on the roof of the branchial chamber in other Gastropoda (*e.g.*, Buccinum and Haliotis). They are termed pallial gills. The only other Molluscs in which they are exactly represented are the curious Opisthobranchs Phyllidia and Pleurophyllidia (fig. 57). In these, as in Patella, the typical ctenidia are aborted, and the branchial function is assumed by close-set lamelliform processes arranged in a series beneath the mantle-skirt on either side of the foot. In fig. 26, *d* the large branchial vein of Patella bringing blood from the gill-series to the heart is seen; where it crosses the series of lamellæ there is a short interval devoid of lamellæ.

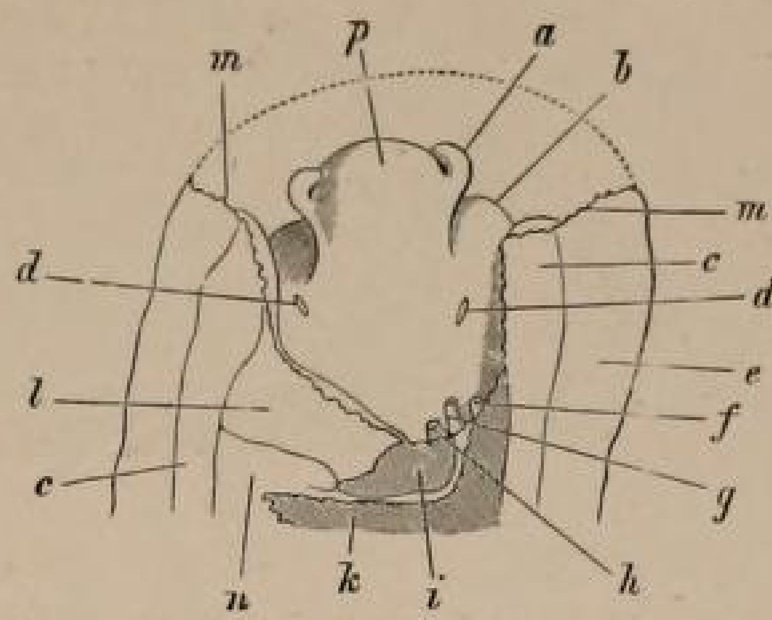


Fig. 28.—Anterior portion of the same Limpet, with the overhanging cephalic hood removed. *a*, cephalic tentacle; *b*, foot; *c*, muscular substance forming the root of the foot; *d*, the capito-pedal organs of Lankester (=rudimentary ctenidia); *e*, mantle-skirt; *f*, papilla of the larger nephridium; *g*, anus; *h*, papilla of the smaller nephridium; *i*, smaller nephridium; *k*, larger nephridium; *l*, pericardium; *m*, cut edge of the mantle-skirt; *n*, liver; *p*, snout. (Original.)

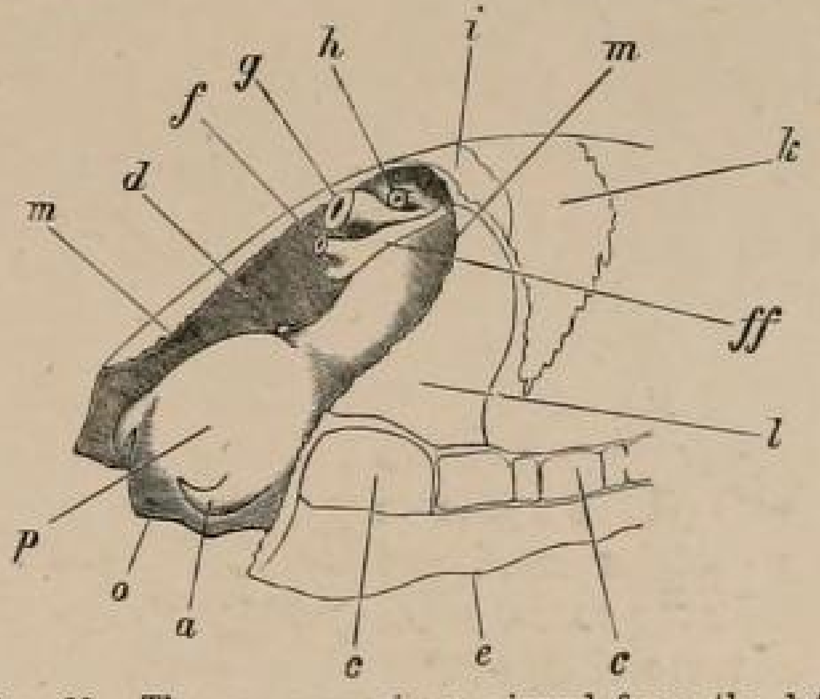


Fig. 29.—The same specimen viewed from the left front, so as to show the sub-anal tract (*ff*) of the larger nephridium, by which it communicates with the pericardium. *o*, mouth; other letters as in fig. 28.

The heart in Patella consists of a single auricle (not two as in Haliotis and Fissurella) and a ventricle; the former receives the blood from the branchial vein, the latter distributes it through a large aorta which soon leads into irregular blood-lacunæ.

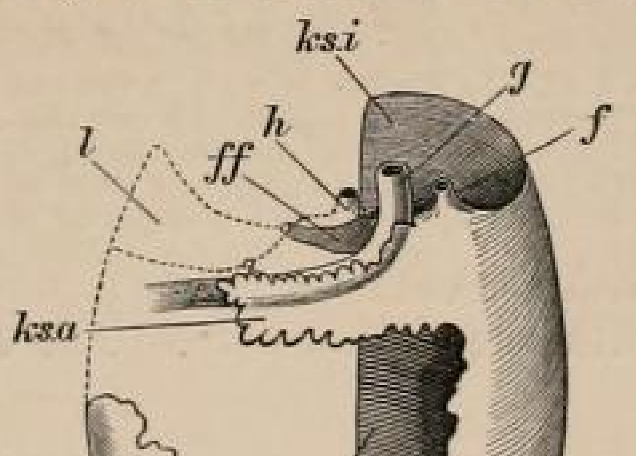


Fig. 30.—Diagram of the two renal organs (nephridia), to show their relation to the rectum and to the pericardium. *f*, papilla of the larger nephridium; *g*, anal papilla with rectum leading from it; *h*, papilla of the smaller nephridium, which is only represented by dotted outlines; *l*, pericardium indicated by a dotted outline,—at its right side are seen the two reno-pericardial pores; *ff*, the sub-anal tract of the large nephridium given off near its papilla and seen through the unshaded smaller nephridium; *ks.a*, anterior superior lobe of the large nephridium; *ks.l*, left lobe of same; *ks.p*, posterior lobe of same; *ks.i*, inferior sub-visceral lobe of same. (Original.)

The existence of two renal organs in Patella, and their relation to the pericardium (a portion of the cœlom), is important. Each renal organ is a sac lined with glandular epithelium (ciliated cells with concretions) communicating with the exterior by its papilla, and by a narrow passage with the pericardium. The connexion with the pericardium of the smaller of the two renal organs was demonstrated by Lankester in 1867, at a time when the fact that the renal organ of the Mollusca, as a rule, opens into the pericardium, and is therefore a typical nephridium, was not known. Subsequent investigations (**27**) carried on under the direction of the same naturalist have shown that the larger as well as the smaller renal sac is in communication with the pericardium. The walls of the renal sacs are deeply plaited and thrown into ridges. Below the surface these walls are excavated with blood-vessels, so that the sac is practically a series of blood-vessels covered with renal epithelium, and forming a mesh-work within a space communicating with the exterior. The larger renal sac (remarkably enough, that which is aborted in other Anisopleura) extends between the liver and the integument of the visceral dome very widely. It also bends round the liver as shown in fig. 30, and forms a large sac on half of the upper surface of the muscular mass of the foot. Here it lies close upon the genital body (ovary or testis), and in such intimate relationship with it that, when ripe, the gonad bursts into the renal sac, and its products are carried to the exterior by the papilla on the right side of the anus (Robin, Dall). This fact led Cuvier erroneously to the belief that a duct existed leading from the gonad to this papilla. The position of the gonad, best seen in the diagrammatic section (fig. 31), is, as in other Zygobranchia, devoid of a special duct communicating with the exterior. This condition, probably an archaic one, distinguishes the Zygobranchia among all Glossophorous Mollusca.

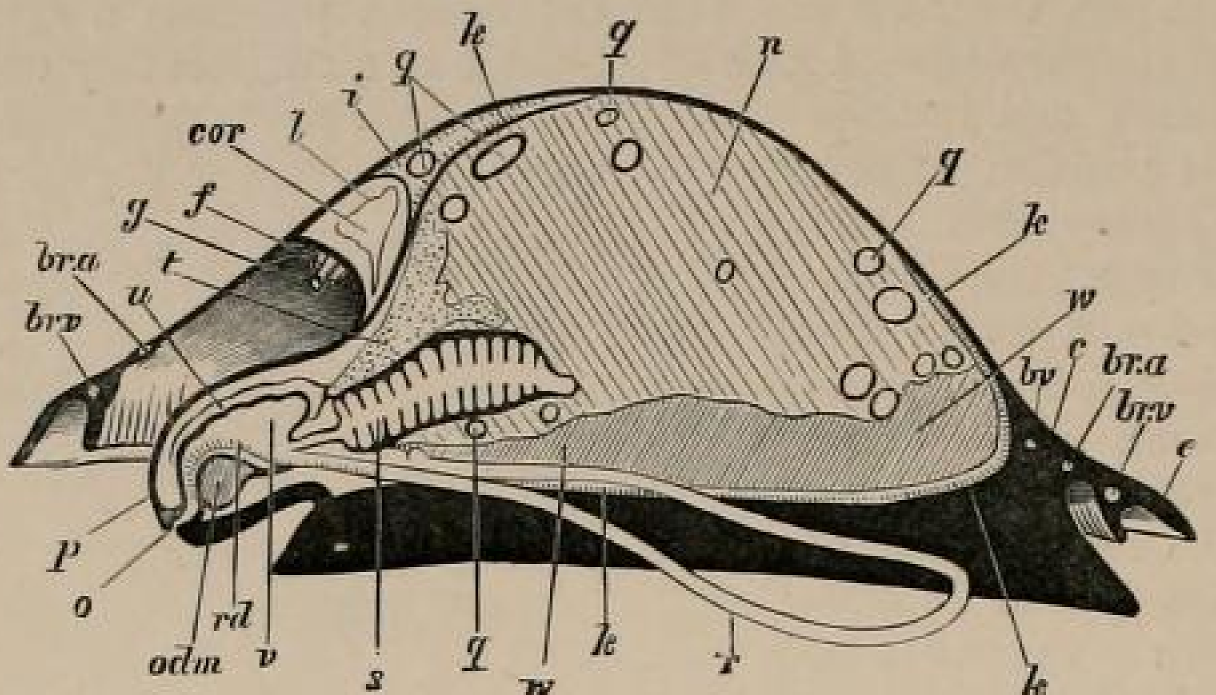


FIG. 31.—Diagram of a vertical antero-postero median section of a Limpet. Letters as in figs. 28, 29, with following additions: *q*, intestine in transverse section; *r*, lingual sac (radular sac); *rd*, radula; *s*, lamellated stomach; *t*, salivary gland; *u*, duct of same; *v*, buccal cavity; *w*, gonad; *br.a*, branchial advehent vessel (artery); *br.v*, branchial efferent vessel (vein); *bv*, blood-vessel; *odm*, muscles and cartilage of the odontophore; *cor*, heart within the pericardium. (Original.)

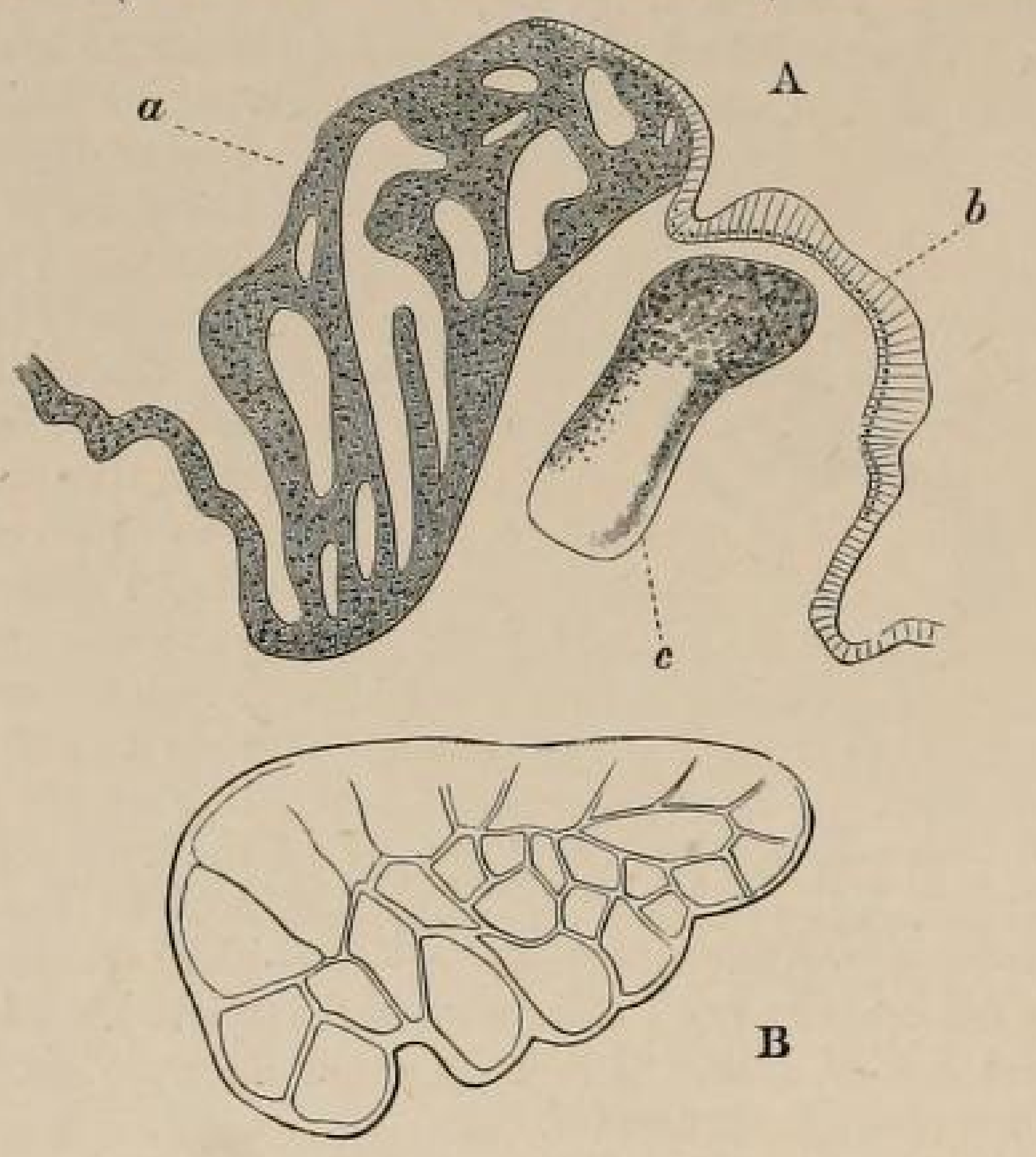


FIG. 32.—A. Section in a plane vertical to the surface of the neck of Patella through *a*, the rudimentary ctenidium (Lankester's organ), and *b*, the olfactory epithelium (osphradium); *c*, the olfactory (osphradial) ganglion. (After Spengel.) B. Surface view of a rudimentary ctenidium of Patella, excised and viewed as a transparent object. (Original.)

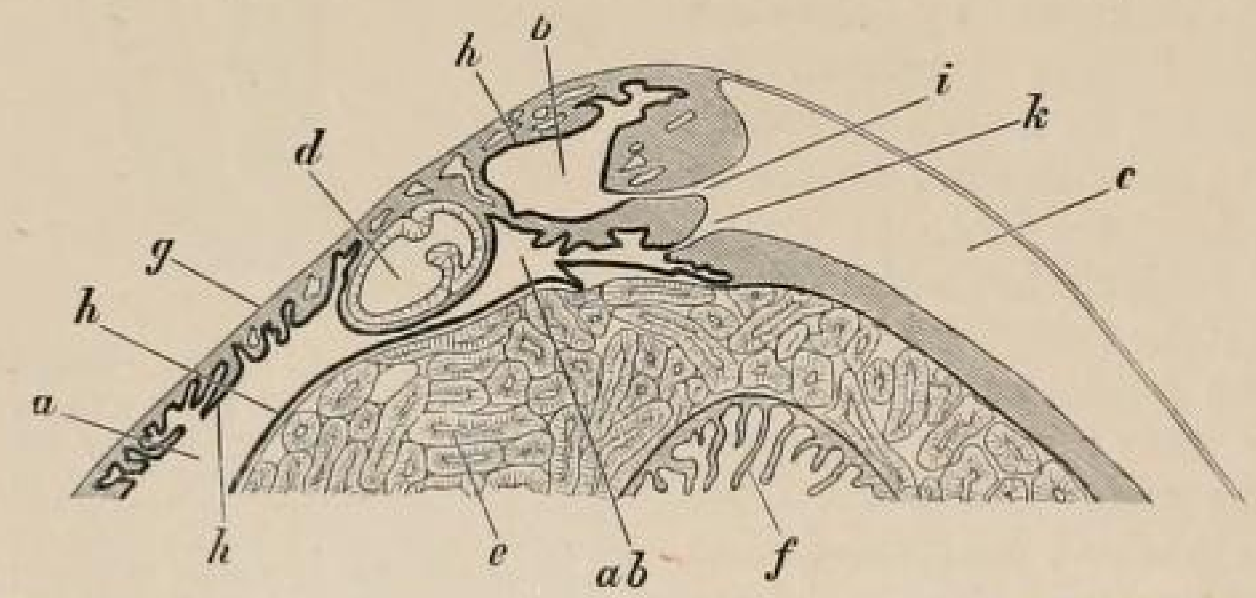


FIG. 33.—Vertical section in a plane running right and left through the anterior part of the visceral hump of Patella, to show the two renal organs and their openings into the pericardium. *a*, large or external or right renal organ; *ab*, narrow process of the same running *below* the intestine and leading by *k* into the pericardium; *b*, small or median renal organ; *c*, pericardium; *d*, rectum; *e*, liver; *f*, manyplies; *g*, epithelium of the dorsal surface; *h*, renal epithelium lining the renal sacs; *i*, aperture connecting the small sac with the pericardium; *k*, aperture connecting the large sac with the pericardium. (From an original drawing by Mr J. T. Cunningham, Fellow of University College, Oxford.)

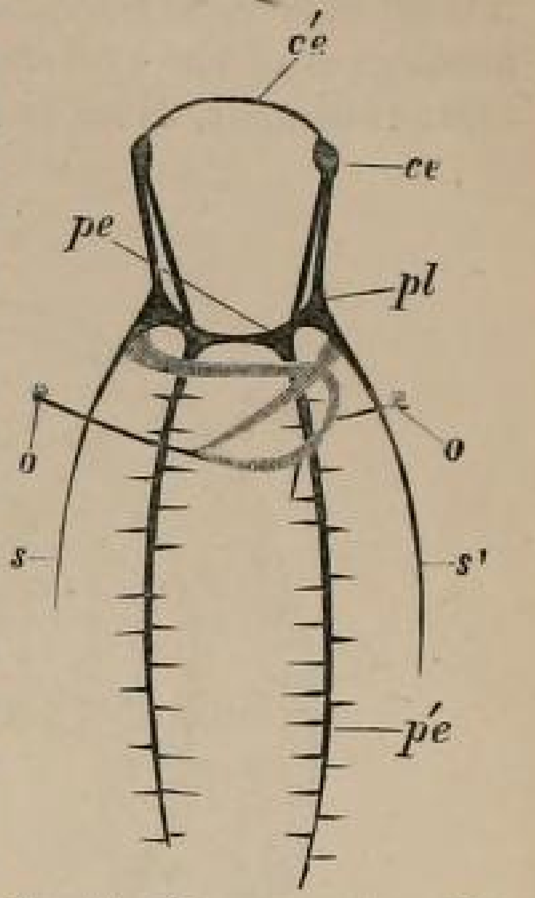


FIG. 34.—Nervous system of Patella; the visceral loop is lightly shaded; the buccal ganglia are omitted. *ce*, cerebral ganglia; *c'e*, cerebral commissure; *pl*, pleural ganglion; *pe*, pedal ganglion; *p'e*, pedal nerve; *s*, *s'*, nerves (right and left) to the mantle; *o*, olfactory ganglion, connected by nerve to the Streptoneurous visceral loop. (After Spengel.)

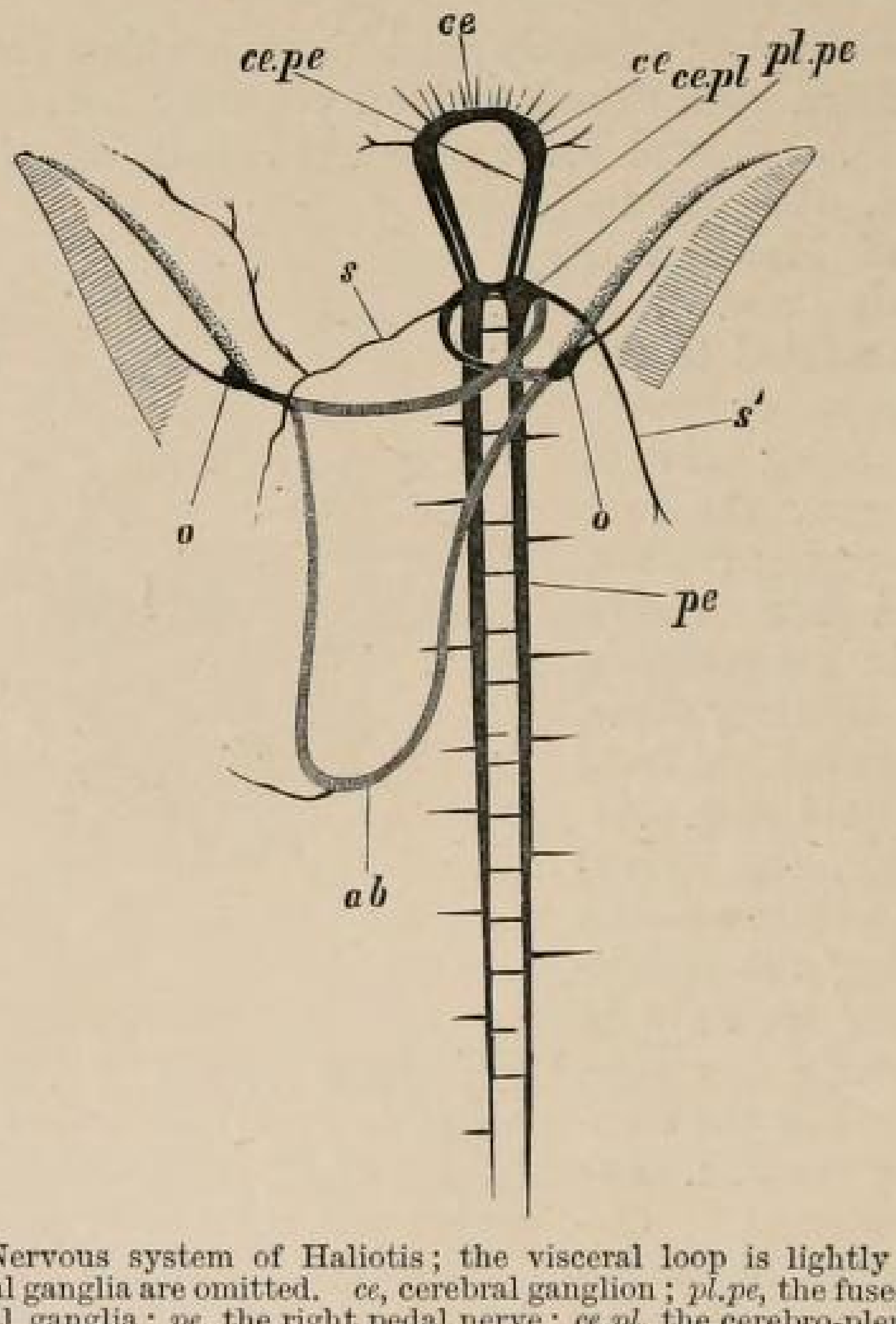


FIG. 35.—Nervous system of Haliotis; the visceral loop is lightly shaded; the buccal ganglia are omitted. *ce*, cerebral ganglion; *pl.pe*, the fused pleural and pedal ganglia; *pe*, the right pedal nerve; *ce.pl*, the cerebro-pleural connective; *ce.pe*, the cerebro-pedal connective; *s*, *s'*, right and left mantle nerves; *ab*, abdominal ganglion or site of same; *o*, *o*, right and left olfactory ganglia and osphradia receiving nerve from visceral loop. (After Spengel.)

The digestive tract of Patella offers some interesting features. The odontophore is powerfully developed; the radular sac is extraordinarily long, lying coiled in a space between the mass of the liver and the muscular foot. The radula has 160 rows of teeth with twelve teeth in each row. Two pairs of salivary ducts, each leading from a salivary gland, open into the buccal chamber. The œsophagus leads into a remarkable stomach, plaited like the manyplies of a sheep, and after this the intestine takes a very large number of turns embedded in the yellow liver, until at last it passes between the two renal sacs to the anal papilla. A curious ridge (spiral? valve) which secretes a slimy cord is found upon the inner wall of the intestine. The general structure of the Molluscan intestine has not been sufficiently investigated to render any comparison of this structure of Patella with that of other Mollusca possible. The eyes of the Limpet (**28**) deserve mention as examples of the most primitive kind of eye in the Molluscan series. They are found one on each cephalic tentacle, and are simply minute open pits or depressions of the epidermis, the epidermic cells lining them being pigmented and connected with nerves (compare fig. 118).

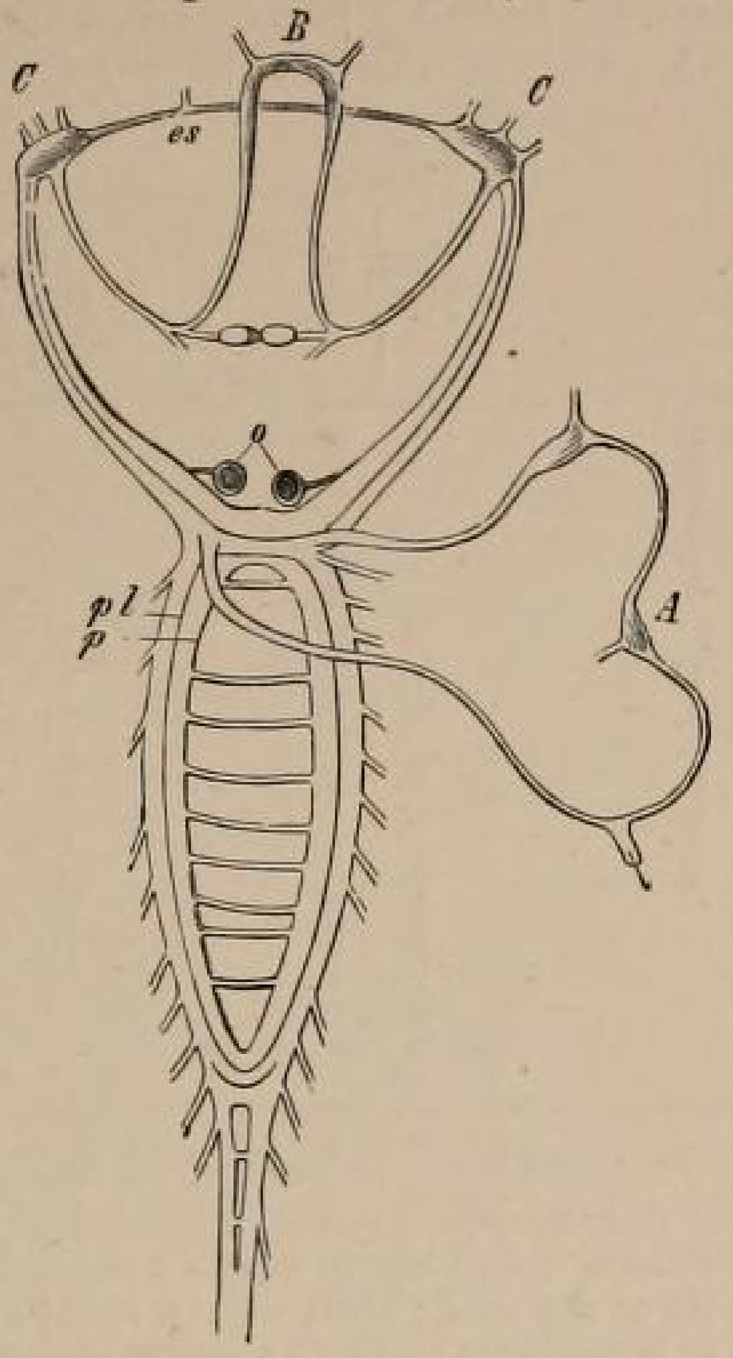


FIG. 36.—Nervous system of Fissurella. *pl*, pallial nerve; *p*, pedal nerve; *A*, abdominal ganglia in the Streptoneurous visceral commissure, with supra- and sub-intestine ganglion on each side; *B*, buccal ganglia; *C*, *C*, cerebral ganglia; *es*, cerebral commissure; *o*, otocysts attached to the cerebro-pedal connectives. (From Gegenbaur, after Jhering.)

The Limpet breeds upon the southern English coast in the early part of April, but its development has not been followed. It has simply been traced as far as the formation of a Diblastula which acquires a ciliated band, and becomes a nearly spherical Trochosphere. It is probable that the Limpet takes several years to attain full growth, and during that period it frequents the same spot, which becomes gradually sunk below the surrounding surface, especially if the rock be carbonate of lime. At low tide the Limpet (being a strictly intertidal organism) is exposed to the air, and is to be found upon its spot of fixation; but when the water again covers it, it (according to trustworthy observers) quits its attachment and walks away in search of food (minute encrusting algæ), and then once more as the tide falls returns to the identical spot, not an inch in diameter, which belongs, as it were, to it. Several million Limpets —twelve million in Berwickshire alone—are annually used on the east coast of Britain as bait.

Order 2.—**Azygobranchia.**

Characters.—Streptoneura which, as a sequel to the torsion of the visceral hump, have lost by atrophy the originally left ctenidium and the originally left nephridium, retaining the right ctenidium as a comb-like gill-plume to the actual left of the rectum, and the right nephridium (that which is the smaller in the Zygobranchia) also to the actual left of the rectum, between it and the gill-plume. The right olfactory organ only is retained, and may assume the form of a comb-like ridge to the actual left of the ctenidium or branchial plume. It has been erroneously described as the second gill, and is known as the parabranchia. The rectum itself lies on the animal's right shoulder. The presence of glandular plication of the surface of the mantle-flap (fig. 46, *x*) and an adrectal gland (purple-gland, fig. 47, *gp*) are frequently observed. The sexes are always distinct; a special genital duct (oviduct or sperm duct) unpaired is present, opening either by the side of the anus or, in the males, on the right side of the neck in connexion with a large penis. The shell is usually large and spiral; often an operculum is developed on the upper surface of the hinder part of the foot. The dentition of the lingual ribbon is very varied. In most cases the visceral hump and the foot increase along axes at right angles to one another, so that the foot is extended far behind the visceral hump in the ab-oral direction, whilst the visceral hump is lofty and spirally twisted.

This is a very large group, and is conveniently divided into two sections, the Reptantia and the Natantia. The former, containing the immense majority of the group, breaks up into three sub-orders, the Holochlamyda, Pneumonochlamyda, and Siphonochlamyda, characterized by the presence or absence of a trough-like prolongation of the margin of the mantle-flap, which conducts water to the respiratory chamber (sub-pallial space where the gill, anus, &c., are placed), and notches the mouth of the shell by its presence, or again by adaptation to aerial respiration. The sub-orders are divided into groups according to the characters of the lingual dentition. In some Azygobranchia the mouth is placed at the end of a more or less elongated snout or rostrum which is not capable of introversion (Rostrifera); in the others (Proboscidifera) the rostrum is partly invaginated and is often of great length. It is only everted when the animal is feeding, and is withdrawn (introverted) by the action of special muscles; the over-worked term "proboscis" is applied to the retractile form of snout. The term "introversible snout," or simply "introvert," would be preferable. The presence or absence of this arrangement does not seem to furnish so natural a division of the Reptant Azygobranchia as that afforded by the characters of the mantle-skirt.

Section *a.*—*REPTANTIA.*

Characters.—Azygobranchia adapted to a creeping life; foot either wholly or only the mesopodium in the form of a creeping disc.

Sub-order 1.—*Holochlamyda.*

Characters.—Reptant Azygobranchia with a simple margin to the mantle-skirt, and, accordingly, the lip of the shell unnotched; mostly Rostrifera (*i.e.*, with a non-introversible snout), and vegetarian; marine, brackish, fresh-water, terrestrial.

α. *Rhipidoglossa* (x.4 to 7.1.4 to 7.x).

Family 1.—*Trochidæ.*
  Genera: *Turbo*, Lin.; *Phasianella*, Lam.; *Imperator*, Montf.; *Trochus*, Lin.; *Rotella*, Lam.; *Euomphalus*, Low.
Family 2.—*Neritidæ.*
  Genera: *Nerita*, L.; *Neritina*, Lam.; *Pileolus*, Low; *Navicella*, Lam.
Family 3.—*Pleurotomaridæ.*
  Genera: *Pleurotomaria*, Defr.; *Anatomus*, Montf.; *Stomatia*, Helbing.

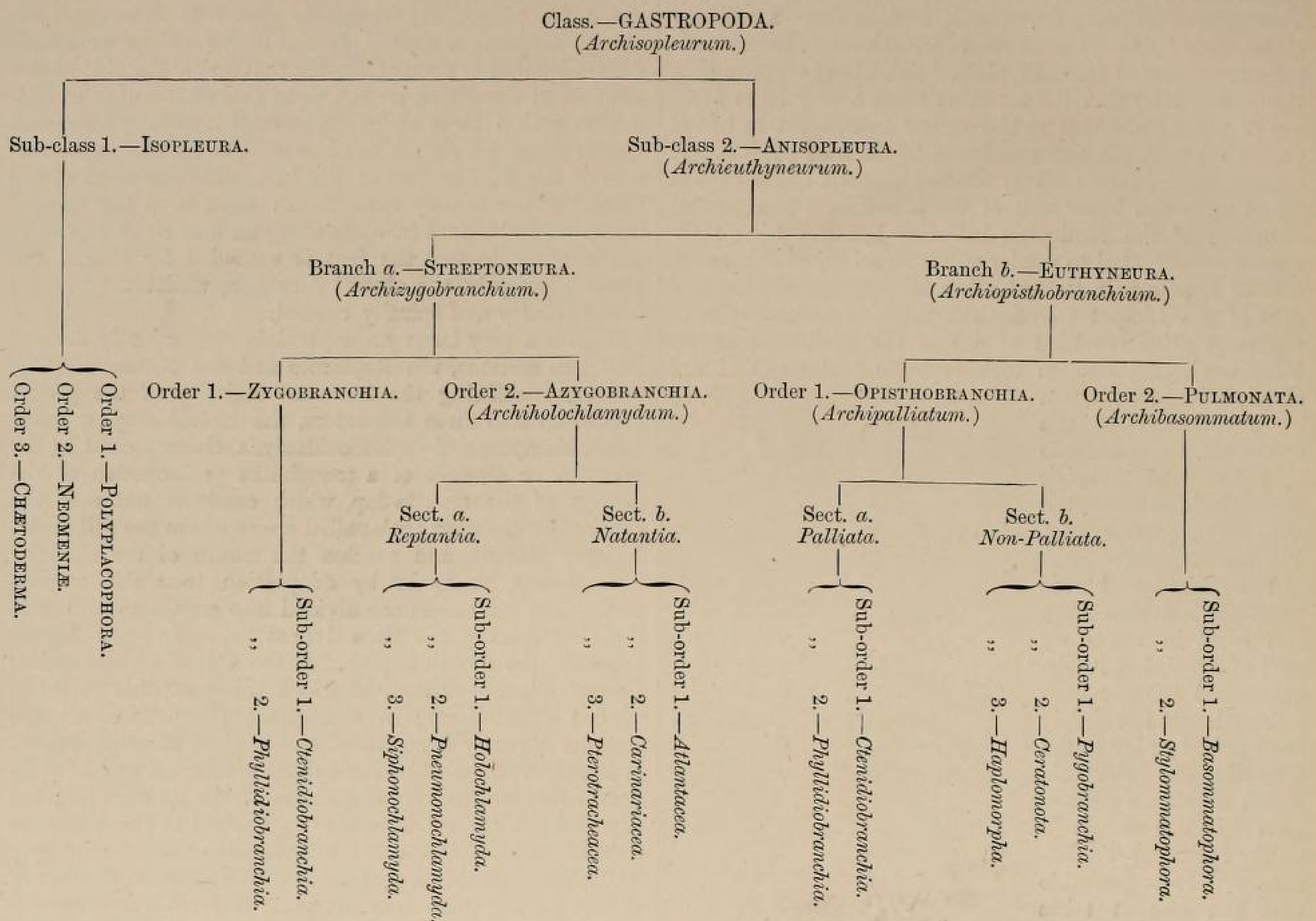
β. *Ptenoglossa* (x.0.x).

Family 4.—*Scalaridæ.*
  Genus: *Scalaria*, Lam.
Family 5.—*Janthinidæ.*
  Genera: *Janthina*, Lam. (fig. 44); *Recluzia*, Petit.

γ. *Tænioglossa* (3.1.3).

Family 6.—*Cerithidæ.*
  Genera: *Cerithium*, Brug.; *Potamides*, Brong.; *Nerinæa*, Defr.
Family 7.—*Melanidæ.*
  Genera: *Melania*, Lam.; *Melanopsis*, Fér.; *Ancylotus*, Lay.
Family 8.—*Pyramidellidæ.*
  Genera: *Pyramidella*, Lam.; *Stylina*, Flem.; *Aclis*, Loven.
Family 9.—*Turritellidæ.*
  Genera: *Turritella*, Lam.; *Cæcum*, Flem.; *Vermetus*, Adans.; *Siliquaria*, Brug.
Family 10.—*Xenophoridæ.*
  Genus: *Phorus*, Montf. (fig. 39).

TABULAR VIEW OF THE SUBDIVISIONS OF THE CLASS GASTROPODA, ARRANGED SO AS TO SHOW THEIR SUPPOSED GENETIC RELATIONSHIPS.



Family 11.—*Naticidæ.*
Genera: *Natica*, Lam.; *Sigaretus*, Lam.; *Neritopsis*, Gratel.

Family 12.—*Entoconchidæ.*
The single genus and species *Entoconcha mirabilis*, discovered by Joh. Müller in 1851, parasitic in *Synapta digitata*. The adult form is not known.

Family 13.—*Marsenidæ.*
Genera: *Marsenia*, Leach; *Onchidiopsis*, Beck.

Family 14.—*Acmæidæ.*
Genera: *Acmæa*, Eschsch.; *Lottia*, Gr.; (probably these will be found to belong to the Zygobranchia).

Family 15.—*Capulidæ.*
Genera: *Capulus*, Montf.; *Calyptræa*, Lam. (fig. 40); *Trochita*, Schum.

Family 16.—*Littorinidæ.*
Genera: *Littorina* (the Periwinkles, fig. 46); *Modulus*, Gray; *Lacuna*, Turt.; *Rissoa*, Frem.; *Hydrobia*, Hartm.; *Assiminia*, Leach.

Family 17.—*Paludinidæ.*
Genera: *Paludina* (River-Snail) (figs. 7, 21); *Bithynia*, Gray; *Tanalia*, Gray.

Family 18.—*Valvatidæ.*
Genus: *Valvata* (fig. 45), fresh-water.

Family 19.—*Ampullaridæ.*
Genus: *Ampullaria* (can breathe air by means of the walls of the pallial chamber as well as water by the gill; fresh-waters of tropical America, Africa, and East Indies).

Sub-order 2.—*Pneumonochlamyda.*

Characters.—Pallial chamber a lung-sac; no gill; mouth on a rostrum, not a retractile proboscis; terrestrial habit.

Family 20.—*Cyclostomidæ.*
Genera: *Cyclostoma*, Lam.; *Cyclophorus*, Montf.; *Ferussina*, Gratel.; *Pupina*, Vignard.

Family 21.—*Helicinidæ* (radula rhipidoglossate rather than tænioglossate).
Genera: *Stoastoma*, Adams; *Trochatella*, Swains.; *Helicina*, Lam.; *Proserpina*, Guild.

Family 22.—*Aciculidæ.*
Genera: *Acicula*, Hartm.; *Geomelania*, Pfr.

Sub-order 3.—*Siphonochlamyda.*

Characters.—Reptant Azygobranchia with the margin of the mantle drawn out to form a trough-like siphon which notches the lip of the shell; shell always spiral; usually an operculum, horny or lamelliform; either a rostrum or a retractile proboscis; exclusively marine; mostly carnivorous.

* *Tænioglossa* (3.1.3).

Family 1.—*Strombidæ.*
Genera: *Strombus*, L.; *Pteroceras*, Lam.; *Rostellaria*, Lam. (fig. 43).

Family 2.—*Aporrhaidæ.*
Genus: *Aporrhais*, Da Costa.

Family 3.—*Pedicularidæ.*
Genus: *Pedicularia*, Swains.

Family 4.—*Dolidæ.*
Genera: *Cassis*, Lam.; *Cassidaria*, Lam.; *Dolium*, Lam.; *Ficula*, Swains.

Family 5.—*Tritonidæ.*
Genera: *Tritonium*, Cuv. (fig. 42); *Ranella*, Lam.

Family 6.—*Cypræidæ* (the Cowries).
Genera: *Cypræa*, L.; *Ovulum*, Brug. (fig. 41); *Erato*, Risso.

* *Toxiglossa* (1.0.1).

Family 7.—*Conidæ.*
Genus: *Conus*, L.

Family 8.—*Terebridæ.*
Genus: *Terebra*, Adans.

Family 9.—*Pleurotomidæ.*
Genus: *Pleurotoma*, Lam.

Family 10.—*Cancellaridæ.*
Genus: *Cancellaria*, Lam.

* *Rachiglossa* (1.1.1 or .1.).

Family 11.—*Muricidæ.*
Genera: *Murex*, L.; *Trophon*, Montf.; *Fusus*, Brug.; *Pyrula*, Lam. (fig. 38); *Turbinella*, Lam.

Family 12.—*Buccinidæ.*
Genera: *Buccinum*, L.; *Nassa*, Lam. (fig. 5); *Purpura*, Brug. (fig. 47); *Concholepas*, Lam.; *Magilus*, Montf.

Family 13.—*Mitridæ.*
Genus: *Mitra*, Lam.

Family 14.—*Olividæ.*
Genera: *Oliva*, Brug.; *Ancilla*, Lam.; *Harpa*, Lam.
Family 15.—*Volutidæ.*
Genera: *Voluta*, L.; *Cymbium*, Montf.; *Marginella*, Lam.; *Volvaria* Lam.

Further Remarks on the Reptant Azygobranchia.—The very large assemblage of forms coming under this order comprise the most highly developed predaceous sea-snails, numerous vegetarian species, a considerable number of fresh-water, and some terrestrial forms. The partial dissection of a male specimen of the Common Periwinkle, *Littorina littoralis*, drawn in fig. 46, will serve to exhibit the disposition of viscera which prevails in the group.

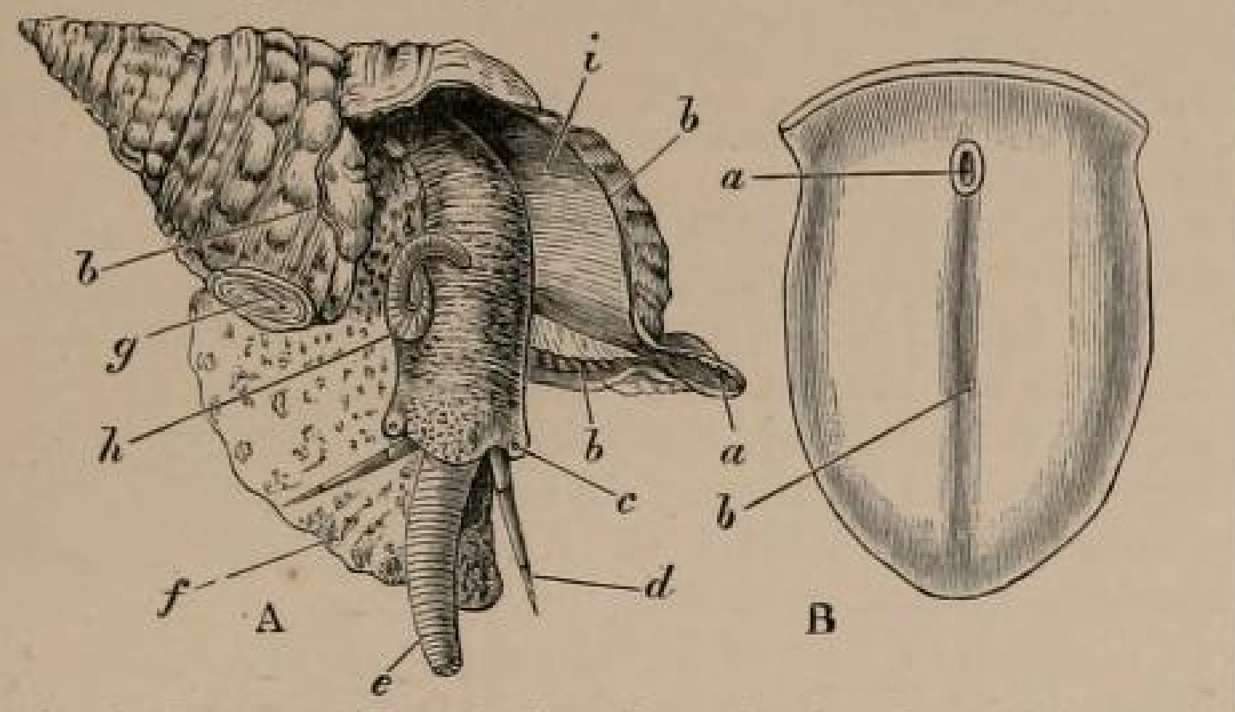


FIG. 37.—A. *Triton variegatum*, to show the proboscis or buccal introvert (*e*) in a state of eversion. *a*, siphonal notch of the shell occupied by the siphonal fold of the mantle-skirt (Siphonochlamyda); *b*, edge of the mantle-skirt resting on the shell; *c*, cephalic eye; *d*, cephalic tentacle; *e*, everted buccal introvert (proboscis); *f*, foot; *g*, operculum; *h*, penis; *i*, under surface of the mantle-skirt forming the roof of the sub-pallial chamber. B. Sole of the foot of *Pyrula tuba*, to show *a*, the pore usually said to be "aquiferous" but probably the orifice of a gland; *b*, median line of foot.

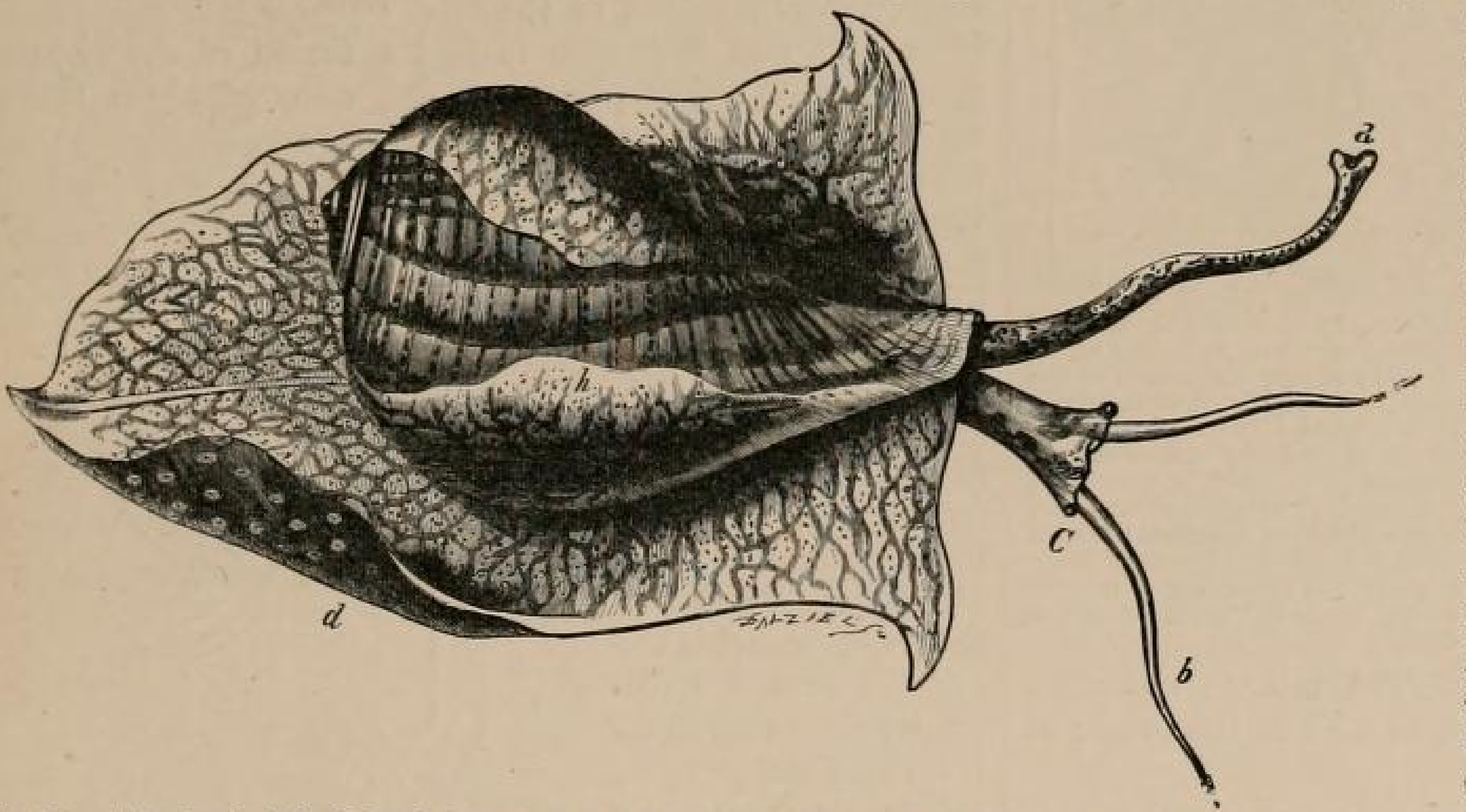


FIG. 38.—Animal and shell of *Pyrula lævigata*. *a*, siphon; *b*, head-tentacles; *C*, head, the letter placed near the right eye; *d*, the foot, expanded as in crawling; *h*, the mantle-skirt reflected over the sides of the shell. (From Owen.

The branchial chamber formed by the mantle-skirt overhanging the head has been exposed by cutting along a line extending backward from the letters *vd* to the base of the columella muscle *mc*, and the whole roof of the chamber thus detached from the right side of the animal's neck has been thrown over to the left, showing the organs which lie upon the roof. No opening into the body-cavity has been made; the organs which lie in the coiled visceral hump show through its transparent walls. The head is seen in front resting on the foot and carrying a median non-retractile snout or rostrum, and a pair of cephalic tentacles at the base of each of which is an eye. In many Gastropoda the eyes are not thus sessile but raised upon special eye-tentacles (figs. 43, 69). To the right of the head is seen the muscular penis *p* close to the termination of the vas deferens (spermatic duct) *vd*. The testis *t* occupies a median position in the coiled visceral mass. Behind the penis on the same side is the hooklike columella muscle, a development of the retractor muscle of the foot, which clings to the spiral column or columella of the shell (see fig. 42). This columella muscle is the same thing as the muscular surface marked *c* in the figures of Patella, marked *k* in fig. 91 of Nautilus, and the posterior adductor of Lamellibranchs (fig. 131).

The surface of the neck is covered by integument forming the floor of the branchial cavity. It has not been cut into.

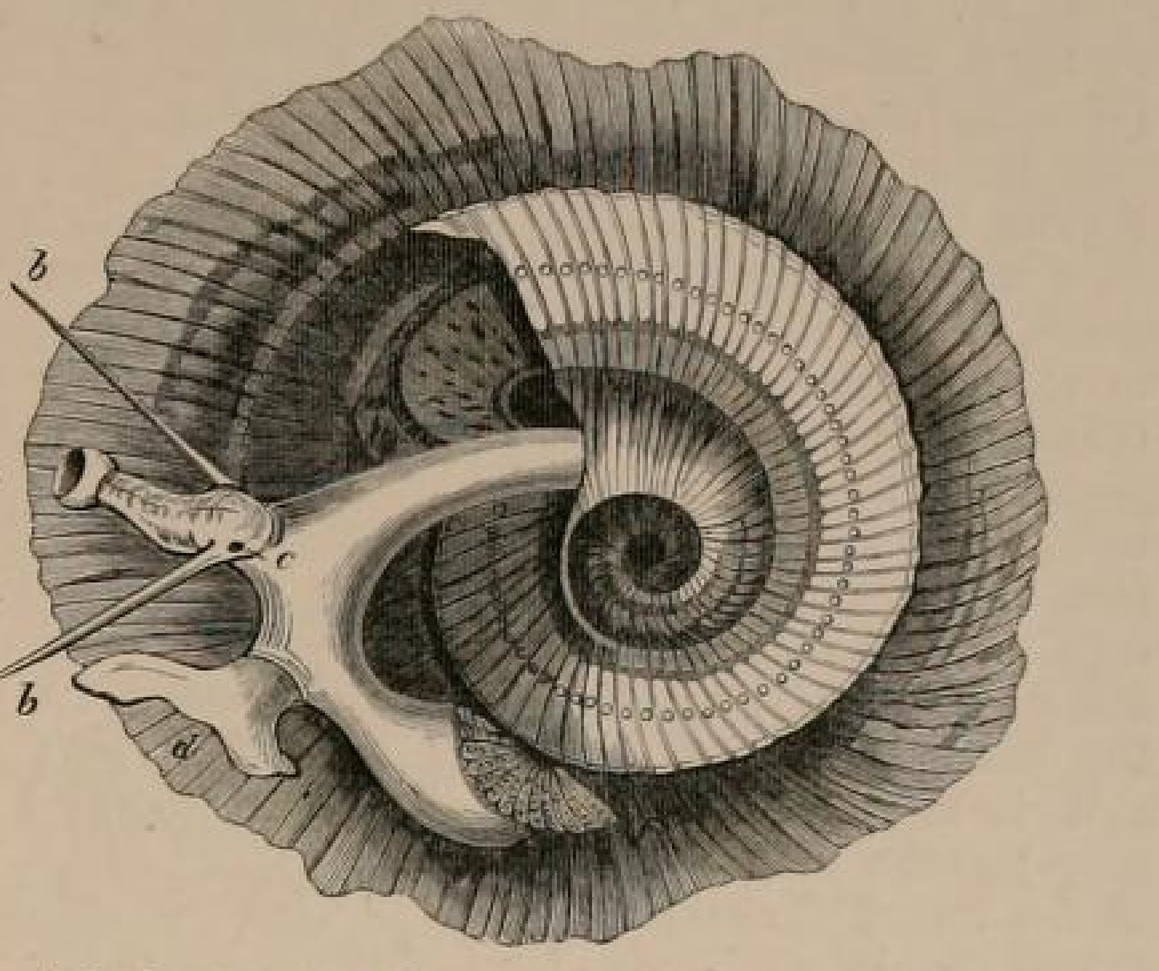


FIG. 39.—Animal and shell of *Phorus exutus*. *a*, snout (not introversible); *b*, cephalic tentacles; *c*, right eye; *d*, pro- and meso-podium,—to the right of this is seen the metapodium bearing the sculptured operculum.

Of the organs lying on the reflected mantle-skirt, that which in the natural state lay nearest to the vas deferens on the right side of the median line of the roof of the branchial chamber is the rectum *i'*, ending in the anus *a*. It can be traced back to the intestine *i* near the surface of the visceral hump, and it is found that the apex of the coil formed by the hump is occupied by the liver *h* and the stomach *v*. Pharynx and œsophagus are concealed in the head. The enlarged glandular structure of the walls of the rectum is frequent in the Azygobranchia, as is also though not universally the gland marked *y*, next to the rectum. It is the adrectal gland, and in the genera Murex and Purpura secretes a colourless liquid which turns purple upon exposure to the atmosphere, and was used by the ancients as a dye. Near this, and less advanced into the branchial chamber, is the single renal organ or nephridium *r* with its opening to the exterior *r'*. Internally this glandular sac presents a second slit or aperture which leads into the pericardium (as is now found to be the case in all Mollusca). The heart *c* lying in the pericardium is seen in close proximity to

FIG. 40.—Shell of Calyptræa, seen from below so as to show the inner whorl *b*, concealed by the caplike outer whorl *a*.

the renal organ, and consists of a single auricle receiving blood from the gill, and of a single ventricle which pumps it through the body by an anterior and posterior aorta (see fig. 105). The surface *x* of the mantle between the rectum and the gill-plume is thrown into folds which in many sea-snails (Whelks, &c.) are very strongly developed. The whole of this surface appears to be active in the secretion of a mucous-like substance. The single gill-plume *br* lies to the left of the median line in natural position. It corresponds to the right of the two primitive ctenidia in the untwisted archaic condition of the Molluscan body, and does not project freely into the branchial cavity, but its axis is attached (by concrescence) to the mantle-skirt (roof of the branchial chamber). It is rare for the gill-plume of an Anisopleurous Gastropod to stand out freely as a plume, but occasionally this more archaic condition is exhibited, as in Valvata (fig. 45). Next beyond (to the left of) the gill-plume we find the so-called parabranchia, which is here simple, but sometimes lamellated as in Purpura (fig. 47). This organ has, without reason, been supposed to represent the second ctenidium of the typical Mollusc, which it cannot do on account of its position. It should be to the right of the anus were this the case. Recently Spengel has shown that the parabranchia of Gastropods is the typical olfactory organ or osphradium in a highly-developed condition The minute structure of the epithelium which clothes it, as well as the origin of the nerve which is distributed to the parabranchia, proves it to be the same organ which is found universally in Molluscs at the base of each gill-plume, and tests the indrawn current of water by the sense of smell. The nerve to this organ is given off from the superior (original right, see fig. 19) visceral ganglion.

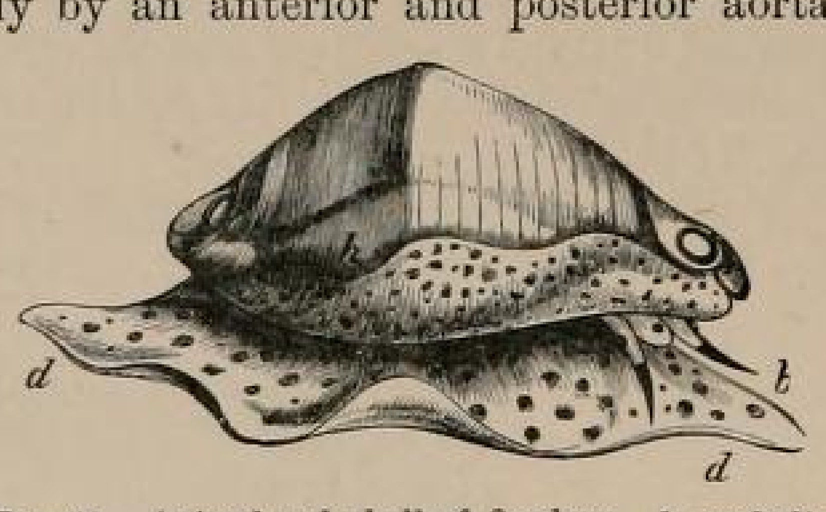


FIG. 41.—Animal and shell of Ovulum. *b*, cephalic tentacles; *d*, foot; *h*, mantle-skirt, which is naturally carried in a reflected condition so as to cover in the sides of the shell.

FIG. 42.—Section of the shell of Tritonium, Cuv. *a*, apex; *ac*, siphonal notch of the mouth of the shell; *ac* to *pc*, mouth of the shell; *w*, *w*, whorls of the shell; *s*, *s*, sutures. Occupying the axis, and exposed by the section, is seen the "columella" or spiral pillar. The upper whorls of the shell are seen to be divided into separate chambers by the formation of successively formed "septa." (From Owen.)

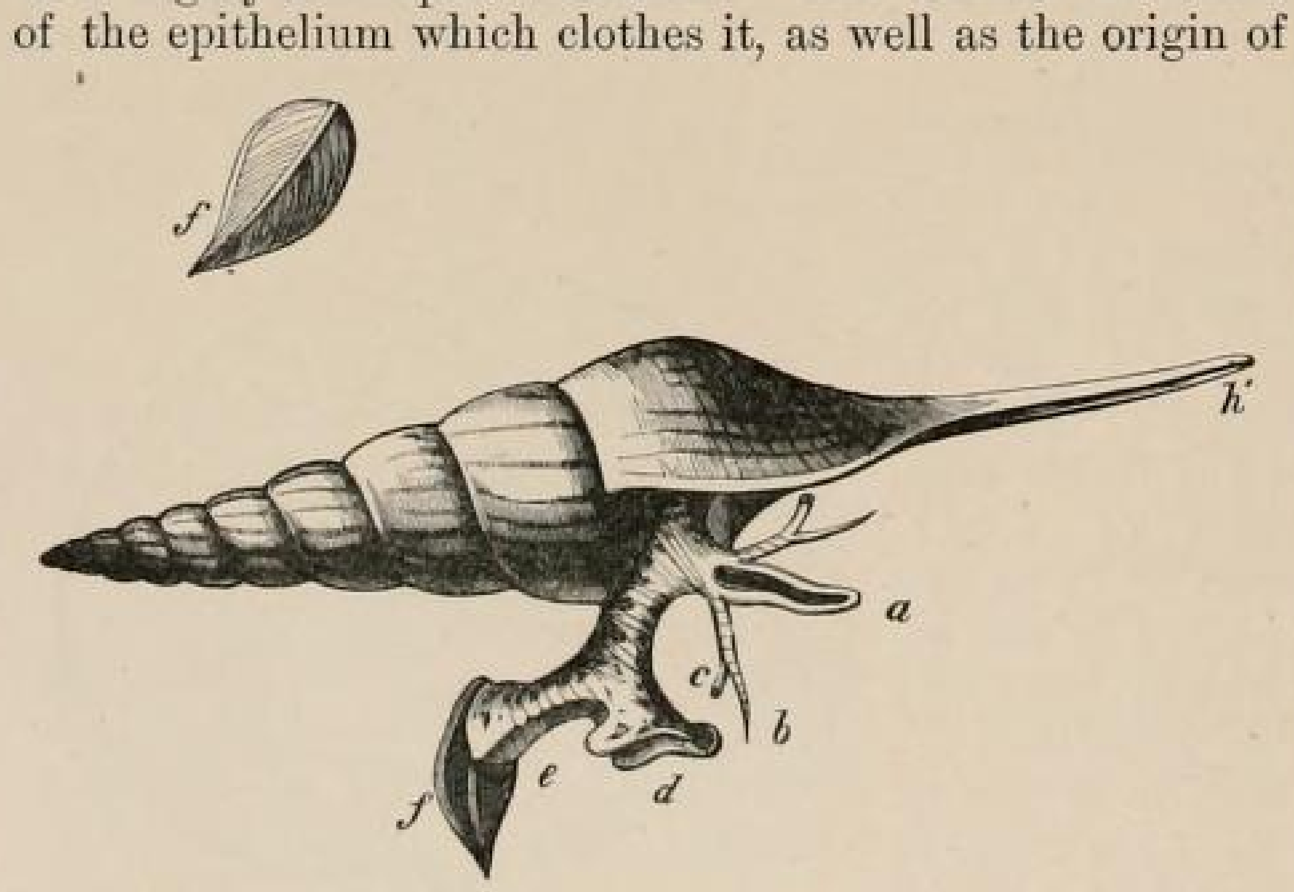


FIG. 43.—Animal and shell of *Rostellaria rectirostris*. *a*, snout or rostrum; *b*, cephalic tentacle; *c*, eye; *d*, propodium and mesopodium; *e*, metapodium; *f*, operculum; *h'*, prolonged siphonal notch of the shell occupied by the siphon, or trough-like process of the mantle-skirt. (From Owen.)

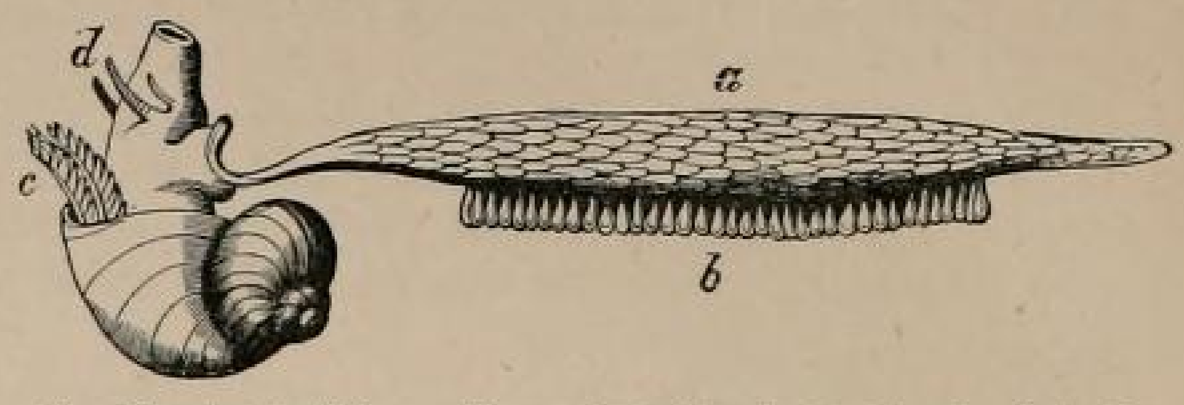


FIG. 44.—Female Janthina, with egg-float (*a*) attached to the foot; *b*, egg-capsules; *c*, ctenidium (gill-plume); *d*, cephalic tentacles.

The figures which are here given of various Azygobranchia are in most cases sufficiently explained by the references attached to them. As an excellent general type of the nervous system, attention may be directed to that of Paludina drawn in fig. 21. On the whole, the ganglia are strongly individualized in the Azygobranchia, nerve-cell tissue being concentrated in the ganglia and absent from the cords (contrast with Zygobranchia and Isopleura). At the same time, the junction of the visceral loop above the intestine prevents in all Streptoneura the shortening of the visceral loop, and it is rare to find a fusion of the visceral ganglia with either pleural, pedal, or cerebral—a fusion which can and does take place where the visceral loop is not above but below the intestine, *e.g.*, in the Euthyneura (fig. 67), Cephalopoda (fig. 112), and Lamellibranchia (fig. 144). As contrasted with the Zygobranchia and the Isopleura, we find that in the Azygobranchia the pedal nerves are distinctly nerves given off from the pedal ganglia, rather than cord-like nerve-tracts containing both nerve-cells or ganglionic elements and nerve-fibres. Yet in some Azygobranchia (Paludina) a ladder-like arrangement of the two pedal nerves and their lateral branches has been detected (**30**). The histology of the nervous system of Mollusca has yet to be seriously inquired into.

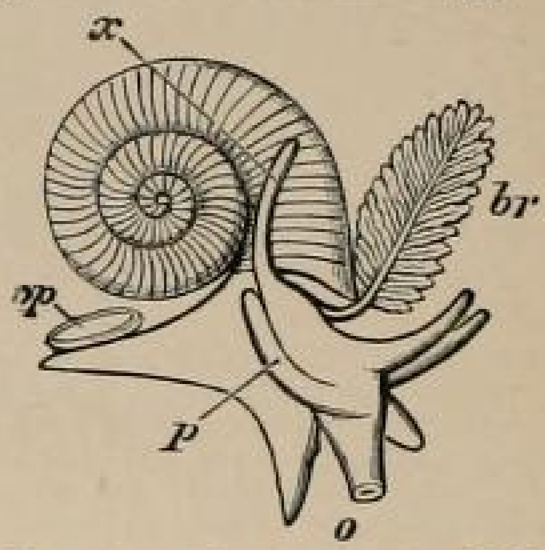


FIG. 45.—*Valvata cristata*, Müll. *o*, mouth; *op*, operculum; *br*, ctenidium (branchial plume); *x*, filiform appendage (? rudimentary ctenidium). The freely projecting ctenidium of typical form not having its axis fused to the roof of the branchial chamber is the notable character of this genus.

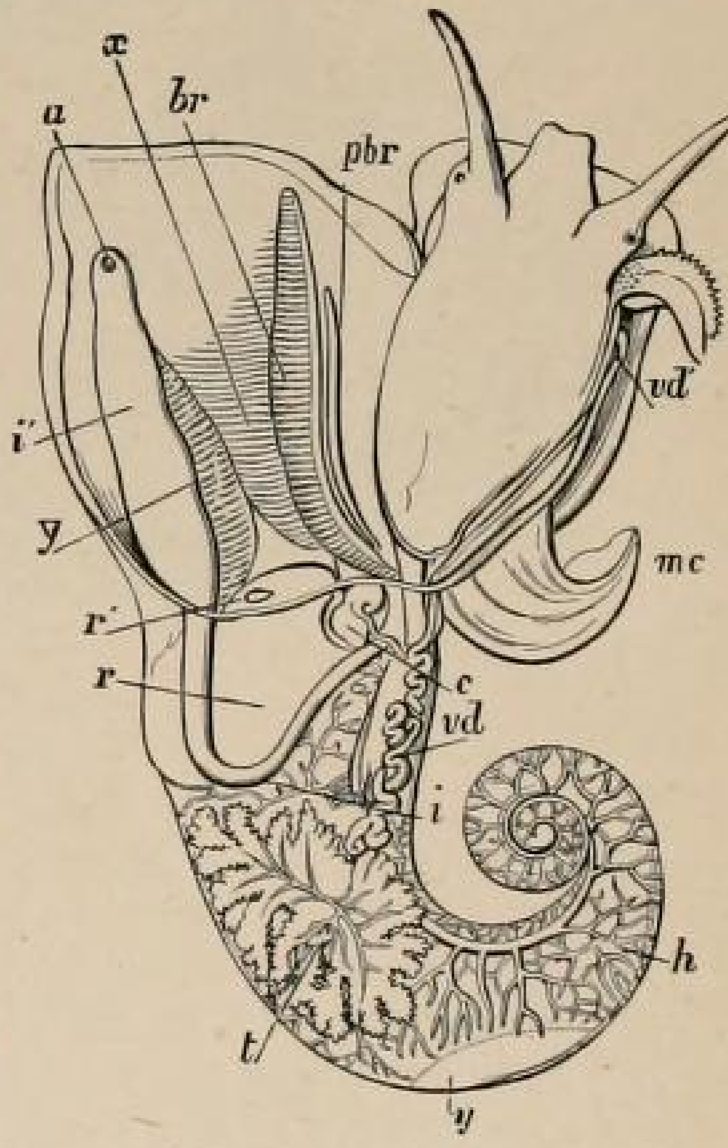


FIG. 46.—Male of *Littorina littoralis*, Lin., removed from its shell; the mantle-skirt cut along its right line of attachment and thrown over to the left side of the animal so as to expose the organs on its inner face. *a*, anus; *i*, intestine; *r*, nephridium (kidney); *r'*, aperture of the nephridium; *c*, heart; *br*, ctenidium (gill-plume); *pbr*, parabranchia (=the osphradium or olfactory patch); *x*, glandular lamellæ of the inner face of the mantle-skirt; *y*, adrectal (purpuriparous) gland; *t*, testis; *vd*, vas deferens; *p*, penis; *mc*, columella muscle (muscular process grasping the shell); *v*, stomach; *h*, liver. *N.B.* Note the simple snout or rostrum not introverted as a "proboscis."

The alimentary canal of the Azygobranchia presents little diversity of character, except in so far as the buccal region is concerned. Salivary glands are present, and in some carnivorous forms (Dolium) these secrete free sulphuric acid (as much as two per cent is present in the secretion), which assists the animal in boring holes by means of its rasping tongue through the shells of other Molluscs upon which it preys. A crop-like dilatation of the gut and a recurved intestine, embedded in the compact yellowish-brown liver, the ducts of which open into it, form the rest of the digestive tract and occupy a large bulk of the visceral hump. The buccal region presents a pair of shelly jaws placed laterally upon the lips, and a wide range of variation in the form of the denticles of the lingual ribbon or radula, the nature of which will be understood by a reference to fig. 9, whilst the systematic list of families given above shows the particular form of dentition characteristic of each division of the order.

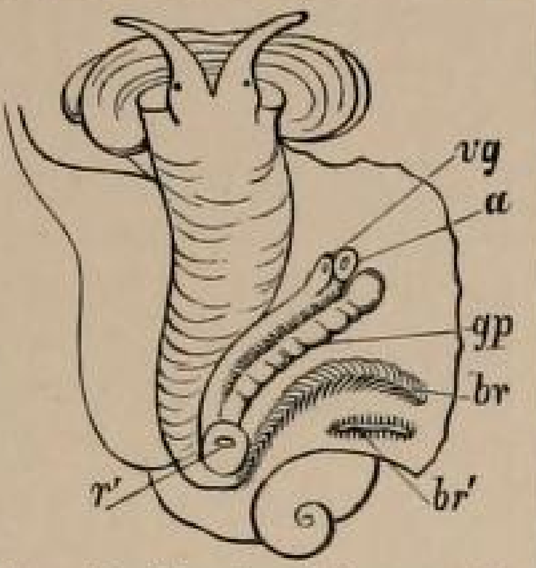


FIG. 47.—Female of *Purpura lapillus* removed from its shell; the mantle-skirt cut along its left line of attachment and thrown over to the right side of the animal so as to expose the organs on its inner face. *a*, anus; *vg*, vagina; *gp*, adrectal purpuriparous gland; *r′*, aperture of the nephridium (kidney); *br*, ctenidium (branchial plume); *br′*, parabranchia (=the comb-like osphradium or olfactory organ).

The modification in the form of the snout upon which the mouth is placed, leading to the distinction of "proboscidiferous" and "rostriferous" Gastropods, requires further notice. The condition usually spoken of as a "proboscis" appears to be derived from the condition of a simple rostrum (having the mouth at its extremity) by the process of *incomplete introversion* of that simple rostrum. There is no reason in the actual significance of the word why the term "proboscis" should be applied to an alternately introversible and eversible tube connected with an animal's body, and yet such is a very customary use of the term. The introversible tube may be completely closed, as in the "proboscis" of Nemertean worms, or it may have a passage in it leading into a non-eversible œsophagus, as in the present case, and in the case of the eversible pharynx of the predatory Chætopod worms. The diagrams here introduced (fig. 48) are intended to show certain important distinctions which obtain amongst the various "introverts," or intro- and e-versible tubes so frequently met with in animal bodies. Supposing the tube to be completely introverted and to commence its eversion, we then find that eversion may take place, either by a forward movement of the side of the tube near its attached base, as in the proboscis of the Nemertine worms, the pharynx of Chætopods, and the eye-tentacle of Gastropods, or, by a forward movement of the inverted apex of the tube, as in the proboscis of the Rhabdocœl Planarians, and in that of Gastropods here under consideration. The former case we call "pleurecbolic" (fig. 48, A, B, C, H, I, K), the latter "acrecbolic" tubes or introverts (fig. 48, D, E, F, G). It is clear that, if we start from the condition of full eversion of the tube and watch the process of introversion, we shall find that the pleurecbolic variety is introverted by the apex of the tube sinking inwards; it may be called acrembolic, whilst conversely the acrecbolic tubes are pleurembolic. Further, it is obvious enough that the process either of introversion or of eversion of the tube may be arrested at any point, by the development of fibres connecting the wall of the introverted tube with the wall of the body, or with an axial structure such as the œsophagus; on the other hand, the range of movement of the tubular introvert may be unlimited or complete. The acrembolic proboscis or frontal introvert of the Nemertine worms has a complete range. So has the acrembolic pharynx of Chætopods, if we consider the organ as terminating at that point where the jaws are placed and the œsophagus commences. So too the acrembolic eye-tentacle of the snail has a complete range of movement, and also the pleurembolic proboscis of the Rhabdocœl prostoma. The introverted rostrum of the Azygobranch Gastropods presents in contrast to these a limited range of movement. The "introvert" in these Gastropods is not the pharynx as in the Chætopod worms, but a præ-oral structure, its apical limit being formed by the true lips and jaws, whilst the apical limit of the Chætopod's introvert is formed by the jaws placed at the junction of pharynx and œsophagus, so that the Chætopod's introvert is part of the stomodæum or fore-gut, whilst that of the Gastropod is external to the alimentary canal altogether, being in front of the mouth, not behind it, as is the Chætopod's. Further, the Gastropod's introvert is pleurembolic (and therefore acrecbolic), and is limited both in eversion and in introversion; it cannot be completely everted owing to the muscular bands (fig. 48, G), nor can it be fully introverted owing to the bands (fig. 48, F) which tie the axial pharynx to the adjacent wall of the apical part of the introvert. As in all such intro- and e-versible organs, eversion of the Gastropod proboscis is effected by pressure communicated by the muscular body-wall to the liquid contents (blood) of the body-space, accompanied by the relaxation of the muscles which directly pull upon either the sides or the apex of the tubular organ. The inversion of the proboscis is effected directly by the contraction of these muscles. In various members of the Azygobranchia the mouth-bearing cylinder is introversible (*i.e.*, is a *proboscis*)—with rare exceptions these forms have a siphonate mantle-skirt. On the other hand, many which have a siphonate mantle-skirt are not provided with an introversible mouth-bearing cylinder, but have a simple non-introversible rostrum, as it has been

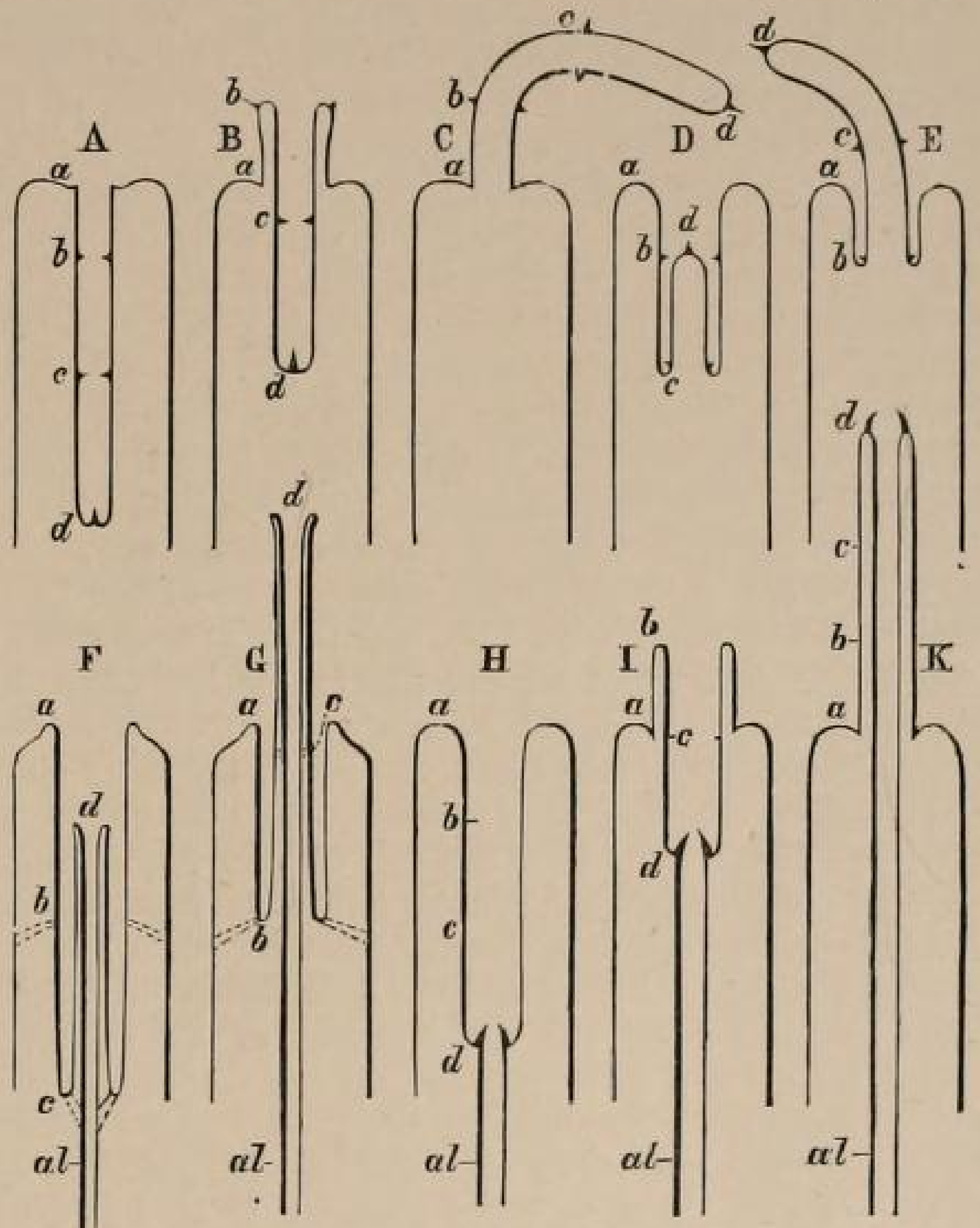


FIG. 48.—Diagrams explanatory of the nature of so-called proboscides or "introverts." A. Simple introvert completely introverted. B. The same, partially everted by eversion of the sides, as in the Nemertine proboscis and Gastropod eye-tentacle=pleurecbolic. C. The same, fully everted. D, E. A similar simple introvert in course of eversion by the forward movement, not of its sides, but of its apex, as in the proboscidean Rhabdocœls=acrecbolic. F. Acrecbolic (=pleurembolic) introvert, formed by the snout of the proboscidiferous Gastropod. *al*, alimentary canal; *d*, the true mouth. The introvert is not a simple one with complete range both in eversion and introversion, but is arrested in introversion by the fibrous bands at *c*, and similarly in eversion by the fibrous bands at *b*. G. The acrecbolic snout of a proboscidiferous Gastropod, arrested short of complete eversion by the fibrous band *b*. H. The acrembolic (=pleurecbolic) pharynx of a Chætopod fully introverted. *al*, alimentary canal; at *d*, the jaws; at *a*, the mouth; therefore *a* to *d* is stomodæum, whereas in the Gastropod (F) *a* to *d* is inverted body-surface. I. Partial eversion of H. K. Complete eversion of H. (Original.)

termed, which is also the condition presented by the mouth-bearing region in nearly all other Gastropoda. One of the best examples of the introversible mouth-cylinder or proboscis which can be found is that of the Common Whelk and its immediate allies. In fig. 37 the proboscis is seen in an everted state; it is only so carried when feeding, being withdrawn when the animal is at rest. Probably its use is to enable the animal to introduce its rasping and licking apparatus into very narrow apertures for the purpose of feeding, *e.g.*, into a small hole bored in the shell of another Mollusc.

The foot of the Azygobranchia, unlike the simple muscular disc of the Isopleura and Zygobranchia, is very often divided into lobes, a fore, middle, and hind lobe (pro-, meso-, and meta-podium, see figs. 39 and 43). Very usually, but not universally, the meta-podium carries an operculum. The division of the foot into lobes is a simple case of that much greater elaboration or breaking up into processes and regions which it undergoes in the class Cephalopoda. Even among some Gastropoda (viz., the Opisthobranchia), we find the lobation of the foot still further carried out by the development of lateral lobes, the epipodia, whilst there are many Azygobranchia, on the other hand, in which the foot has a simple oblong form without any trace of lobes.

The development of the Azygobranchia from the egg has been followed in several examples, *e.g.*, Paludina, Purpura, Nassa, Vermetus, Neritina. As in other Molluscan groups, we find a wide variation in the early process of the formation of the first embryonic cells, and their arrangement as a Diblastula dependent on the greater or less amount of food-yelk which is present in the egg-cell when it commences its embryonic changes. In fig. 7, the early stages of *Paludina vivipara* are represented. There is but very little food-material in the egg of this Azygobranch, and consequently the Diblastula forms by invagination; the blastopore or orifice of invagination coincides with the anus, and never closes entirely. A well-marked Trochosphere is formed by the development of an equatorial ciliated band; and subsequently, by the disproportionate growth of the lower hemisphere, the Trochosphere becomes a Veliger. The primitive shell-sac or shell-gland is well marked at this stage, and the pharynx is seen as a new ingrowth (the stomodæum), about to fuse with and open into the primitively invaginated arch-enteron (fig. 7, F).

In other Azygobranchs (and such variations are representative for all Mollusca, and not characteristic only of Azygobranchia), we find that there is a very unequal division of the egg-cell at the commencement of embryonic development, as in Nassa (fig. 5). Consequently there is strictly speaking no invagination (emboly), but an overgrowth (epiboly) of the smaller cells to enclose the larger. The general features of this process and of the relation of the blastopore to mouth and anus have been explained above in treating of the development of Mollusca generally. In such cases the blastopore may entirely close, and both mouth and anus develop as new ingrowths (stomodæum and proctodæum), whilst, according to the observations of Bobretzky, the closed blastopore may coincide in position with the mouth in some instances (Nassa, &c.), instead of with the anus. But in these epibolic forms, just as in the embolic Paludina, the embryo proceeds to develop its ciliated band and shell-gland, passing through the earlier condition of a Trochosphere to that of the Veliger. In the veliger stage many Azygobranchia (Purpura, Nassa, &c.) exhibit, in the dorsal region behind the head, a contractile area of the body-wall. This acts as a larval heart, but ceases to pulsate after a time. Similar rhythmically contractile areas are found on the foot of the embryo Pulmonate Limax and on the yelk-sac (distended foot-surface) of the Cephalopod Loligo (see fig. 72**).

The history of the shell in the development of Azygobranchia (and other Gastropods) is important. Just as the primitive shell-sac aborts and gives place to a cap-like or boat-like shell, so in some cases (Marsenia, Krohn) has this first shell been observed to be shed, and a second shell of different shape is formed beneath it.

A detailed treatment of what is known of the histogenesis in relation to the cell-layers in these Mollusca would take us far beyond the limits of this article, which aims at exposing only the well-ascertained characteristic features of the Mollusca and the various subordinate groups. There is still a great deficiency in our knowledge of the development of the Gastropoda, as indeed of all classes of animals. The development of the gill (ctenidium) as well as of the renal organ, and details as to the process of torsion of the visceral hump, are still quite insufficiently known.

One further feature of the development of the Azygobranchia deserves special mention. Many Gastropoda deposit their eggs, after fertilization, enclosed in capsules; others, as Paludina, are viviparous; others, again, as the Zygobranchia, agree with the Lamellibranch Conchifera (the Bivalves) in having simple exits for the ova without glandular walls, and therefore discharge their eggs unenclosed in capsules freely into the sea-water; such unencapsuled eggs are merely enclosed each in its own delicate chorion. When egg-capsules are formed they are often of large size, have tough walls, and in each capsule are several eggs floating in a viscid fluid. In some cases all the eggs in a capsule develop; in other cases one egg only in a capsule (Neritina), or a small proportion (Purpura, Buccinum), advance in development; the rest are arrested either after the first process of cell-division (cleavage) or before that process. The arrested embryos or eggs are then swallowed and digested by those in the same capsule which have advanced in development. The details of this history require renewed study, our present knowledge of it being derived from the works of Koren and Danielssen, Carpenter and Claparède. In any case it is clearly the same process in essence as that of the formation of a vitellogenous gland from part of the primitive ovary, or of the feeding of an ovarian egg by the absorption of neighbouring potential eggs; but here the period at which the sacrifice of one egg to another takes place is somewhat late. What it is that determines the arrest of some eggs and the progressive development of others in the same capsule is at present unknown.

Section *b* (of the Azygobranchia).—*NATANTIA.*

Characters.—Azygobranchiate Streptoneura which have the form and texture of the body adapted to a free-swimming pelagic habit. They appear to be derived from holochlamydic forms of Reptant Azygobranchia. The foot takes the form of a swimming organ. The nervous system and sense-organs (eyes, otocysts, and osphradium) are highly developed. The odontophore also is remarkably developed, its admedian teeth being mobile, and it serves as an efficient organ for attacking other pelagic forms upon which the Natantia prey. The sexes are distinct as in all Streptoneura; and genital ducts and accessory glands and pouches are present as in all Azygobranchia. The Natantia exhibit a series of modifications of the form and proportions of the visceral mass and foot, leading from a condition readily comparable with that of a typical Azygobranch such as Rostellaria, with the three regions of the foot (pro-, meso-, and meta-podium) strongly marked, and a coiled visceral hump of the usual proportions, up to a condition in which the whole body is of a tapering cylindrical shape, the foot a plate-like vertical fin, and the visceral hump almost completely atrophied. Three steps of this modification may be distinguished as three sub-orders, the *Atlantacea*, the *Carinariacea*, and the *Pterotracheacea.*

Sub-order 1.—*Atlantacea.*

Characters.—Natantia with a large spirally-wound visceral hump, covered by a hyaline spiral shell; mantle-skirt large, overhanging a well-developed sub-pallial branchial chamber as in Azygobranchia, to the wall of which is attached the branchial ctenidium; foot well developed, divisible into a mobile propodium, a mesopodium on which is formed a sucker, and a metapodium which, when the animal is expanded, extends backwards beyond the shell and visceral hump; upon the upper surface of the metapodium is developed an operculum.

Genera: *Atlanta, Oxygurus.* Probably here belong the Palæozoic fossils *Bellerophon.*

Sub-order 2.—*Carinariacea.*

Characters.—Visceral hump greatly reduced in relative size; shell small, cap-like, hyaline; ctenidium (branchial plume) projecting from the small sub-pallial chamber; body cylindrical; of the foot-lobes only the mesopodium is prominent, provided with a sucker, and compressed laterally so as to form a vertical plate-like fin projecting from the ventral surface; the propodium forms simply the ventral surface of the anterior region of the cylindrical body whilst the metapodium forms its posterior region.

Genera: *Carinaria, Cardiopoda.*

Sub-order 3.—*Pterotracheacea.*

Characters.—Visceral hump still further reduced, forming a mere oval sac embedded in the posterior dorsal region of the cylindrical body; no shell; foot as in Carinariacea, except that the sucker is absent from the mesopodium in the females.

Genera: *Pterotrachea, Firuloides.*

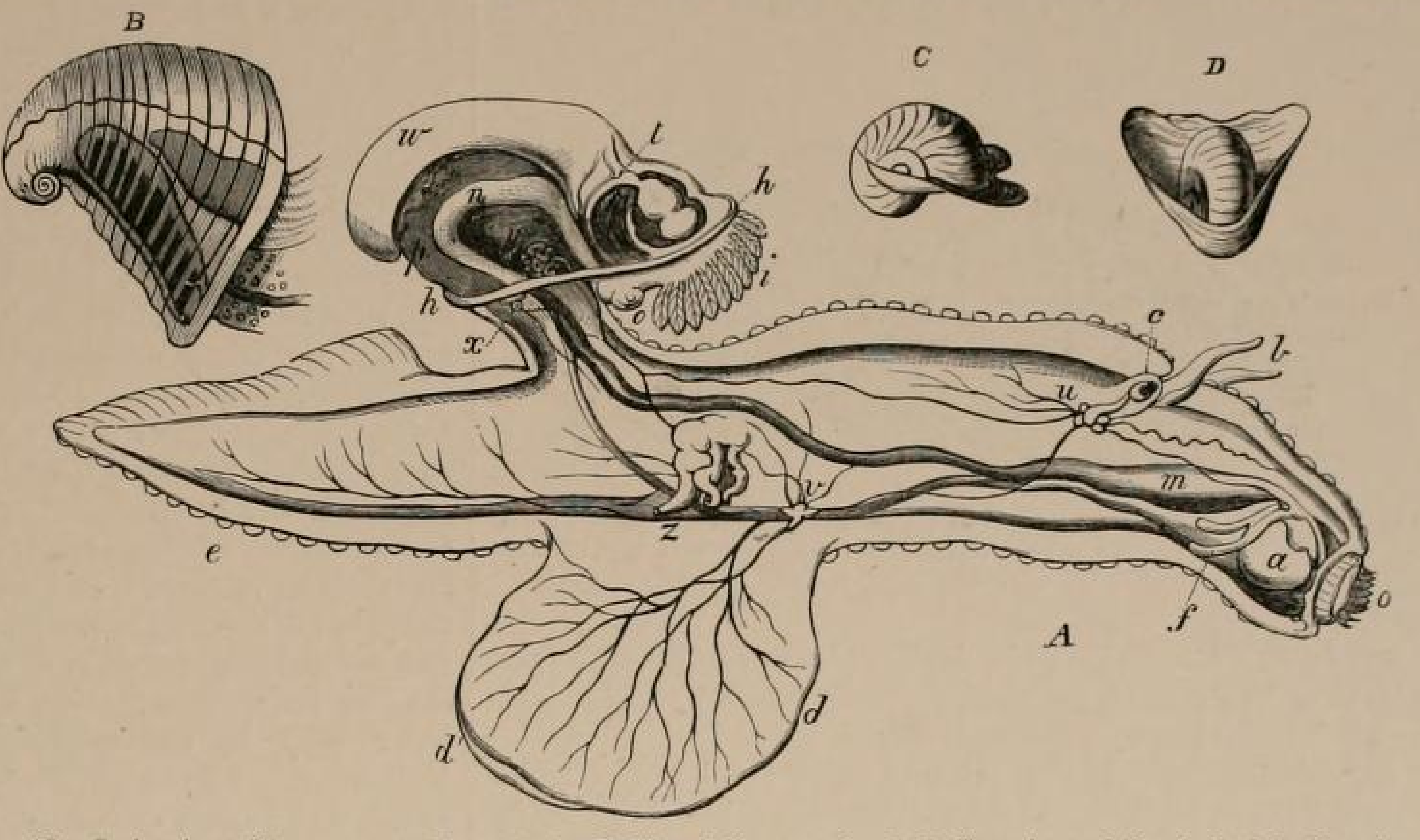


FIG. 50.—*Carinaria mediterranea.* A. The animal. B. The shell removed. C, D. Two views of the shell of Cardiopoda. *a*, mouth and odontophore; *b*, cephalic tentacles; *c*, eye; *d*, the fin-like mesopodium; *d′*, its sucker; *e*, metapodium; *f*, salivary glands; *h*, border of the mantle-flap; *i*, ctenidium (gill-plume); *m*, stomach; *n*, intestine; *o*, anus; *p*, liver; *t*, aorta, springing from the ventricle; *u*, cerebral ganglion; *v*, pleural and pedal ganglion; *w*, testis; *x*, visceral ganglion; *y*, vesicula seminalis; *z*. penis. (From Owen.)

Further Remarks on the Natantia Azygobranchia.—Logically the Natantia should stand as we have placed them, viz., as a special branch or section of the Azygobranchia, related to them somewhat as are the Birds to the Reptiles. They are true Azygobranchia which have taken to a pelagic life, and the peculiarities of structure which they exhibit are strictly adaptations of the structure common to them and the Azygobranchia consequent upon their changed mode of life. Such adaptations are the transparency and colourlessness of the tissues, and the modifications of the foot, which still shows in Atlanta the form common in Azygobranchia (compare fig. 49 and fig. 39).

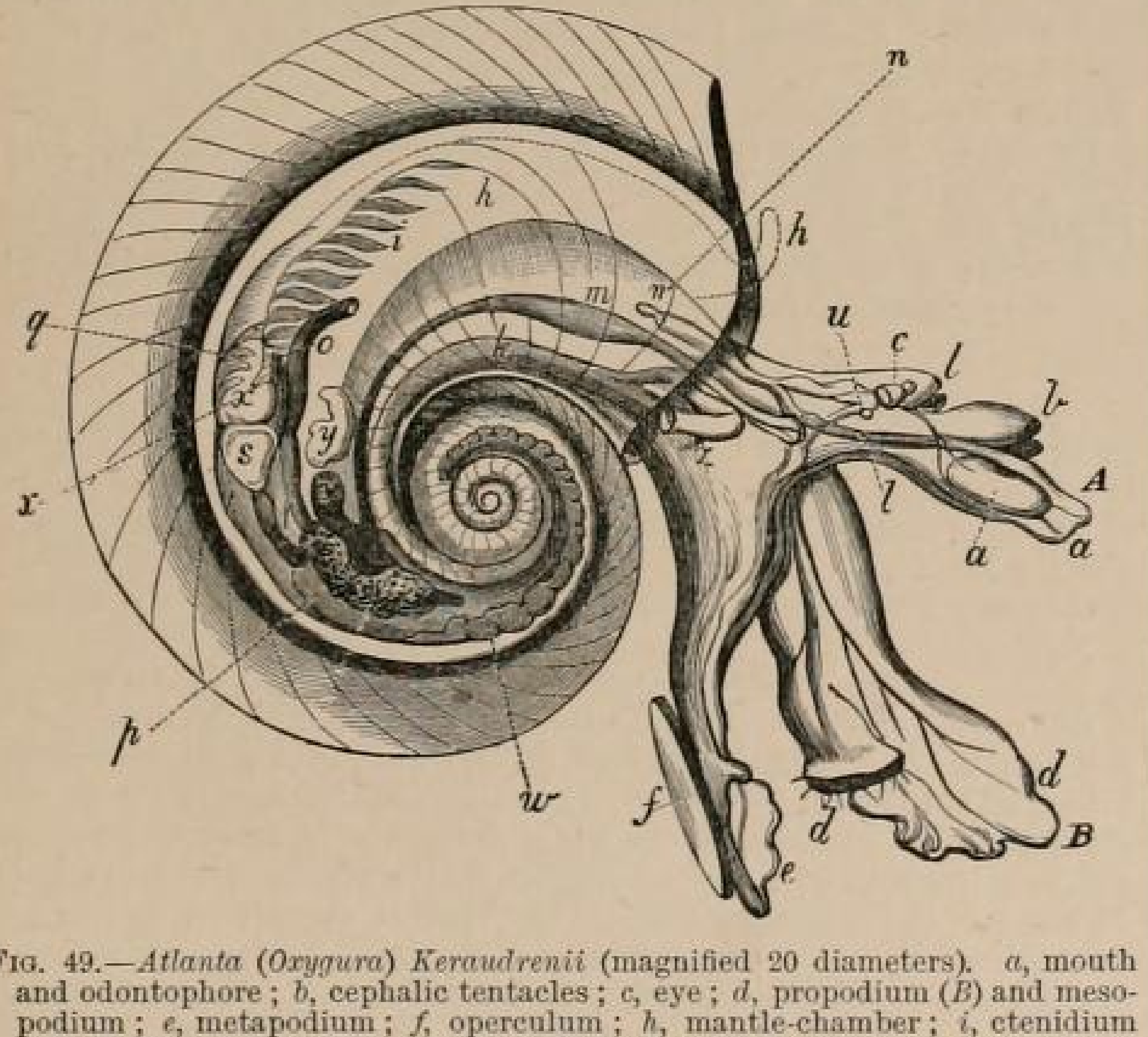


FIG. 49.—*Atlanta (Oxygura) Keraudrenii* (magnified 20 diameters). *a*, mouth and odontophore; *b*, cephalic tentacles; *c*, eye; *d*, propodium (*B*) and mesopodium; *e*, metapodium; *f*, operculum; *h*, mantle-chamber; *i*, ctenidium (gill-plume); *k*, retractor muscle of foot; *l*, optic tentacle; *m*, stomach; *n*, dorsal surface overhung by the mantle-skirt, the letter is close to the salivary gland; *o*, rectum and anus; *p*, liver; *q*, renal organ (nephridium); *s*, ventricle; *u*, the otocyst attached to the cerebral ganglion; *w*, testis; *x*, auricle of the heart; *y*, vesicle on genital duct; *z*, penis. (From Owen.)

The cylindrical body of Pterotracheacea is paralleled by the slug-like forms of Euthyneura. Spengel has shown that the visceral loop of the Natantia is Streptoneurous. Special to the Natantia is the high elaboration of the lingual ribbon, and, as an agreement with some of the Opisthobranchiate Euthyneura but as a difference from the Azygobranchia, we find the otocysts closely attached to the cerebral ganglia. This is, however, less of a difference than it was at one time supposed to be, for it has been shown by Lacaze Duthiers, and also by Leydig, that the otocysts of Azygobranchia even when lying close upon the pedal ganglion (as in fig. 21) yet receive their special nerve (which can sometimes be readily isolated) from the cerebral ganglion (see fig. 36). Accordingly the difference is one of position of the otocyst and not of its nerve-supply. The Natantia are further remarkable for the high development of their cephalic eyes, and for the typical character of their osphradium (Spengel's olfactory organ). This is a groove, the edges of which are raised and ciliated, lying near the branchial plume in the genera which possess that organ, whilst in Firuloides, which has no branchial plume, the osphradium occupies a corresponding position. Beneath the ciliated groove is placed an elongated ganglion (olfactory ganglion) connected by a nerve to the supra-intestinal (therefore the primitively dextral) ganglion of the long visceral nerve-loop, the strands of which cross one another,—this being characteristic of Streptoneura (Spengel).

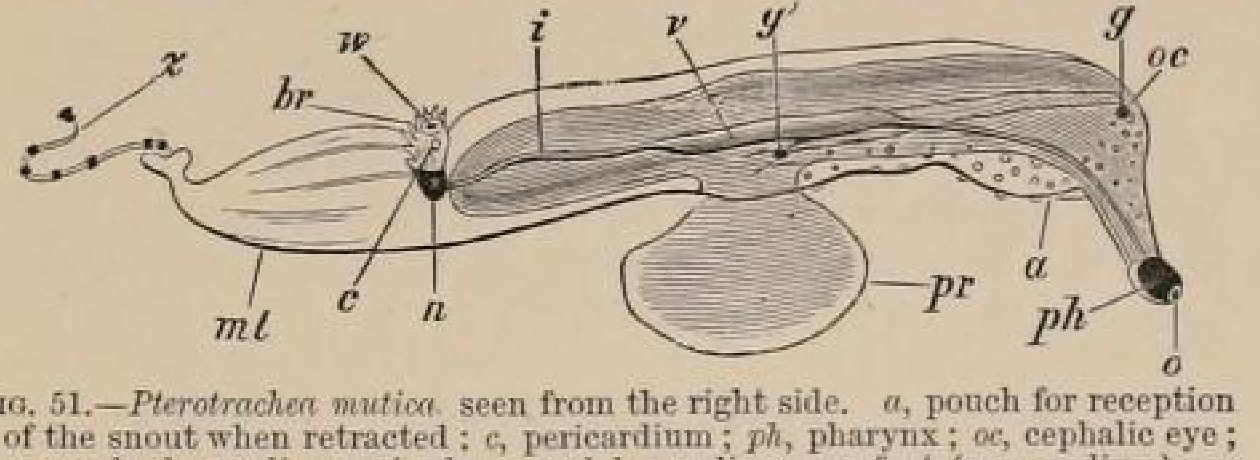


FIG. 51.—*Pterotrachea mutica* seen from the right side. *a*, pouch for reception of the snout when retracted; *c*, pericardium; *ph*, pharynx; *oc*, cephalic eye; *g*, cerebral ganglion; *g′*, pleuro-pedal ganglion; *pr*, foot (mesopodium); *v*, stomach; *i*, intestine; *n*, so-called nucleus; *br*, branchial plume (ctenidium); *w*, osphradium; *mt*, foot (metapodium); *z*, caudal appendage. (After Keferstein.)

The Natantia belong to the "pelagic fauna" occurring near the surface in the Mediterranean and great oceans in company with the Pteropoda, the Siphonophorous Hydrozoa, Salpæ, Leptocephali, and other specially-modified transparent swimming representatives of various groups of the animal kingdom. In development they pass through the typical trochosphere and veliger stages provided with boat-like shell.

Branch *b*.—*EUTHYNEURA* (Spengel, 1881).

Characters. — Gastropoda Anisopleura in which the visceral loop (the conterminous visceral nerves) does not share in the torsion of the visceral hump, but, being sunk entirely below the body-wall, remains straight and untwisted. Although the anus is not brought so far forward by the visceral torsion as in the Streptoneura, and may even by *secondary* growth assume a posterior median position, yet, as fully developed, an asymmetry has resulted as in the Azygobranchia, only the original right renal organ, right ctenidium (if any), right osphradium, right side of the heart, and right genital ducts being retained. All the Euthyneura are hermaphrodite. The lingual ribbon has very usually numerous fine denticles undifferentiated into series in each row. The shell is light and little calcified; often it is not developed in the adult, though present in the embryo. An operculum, often found in the embryo, is never present in the adult (except in Tornatella, fig. 53). Many Euthyneura show a tendency to, or a complete accomplishment of, the suppression of the mantle-skirt as well as of the shell, also of the ctenidium, and acquire at the same time a more or less cylindrical (slug-like) form of body.

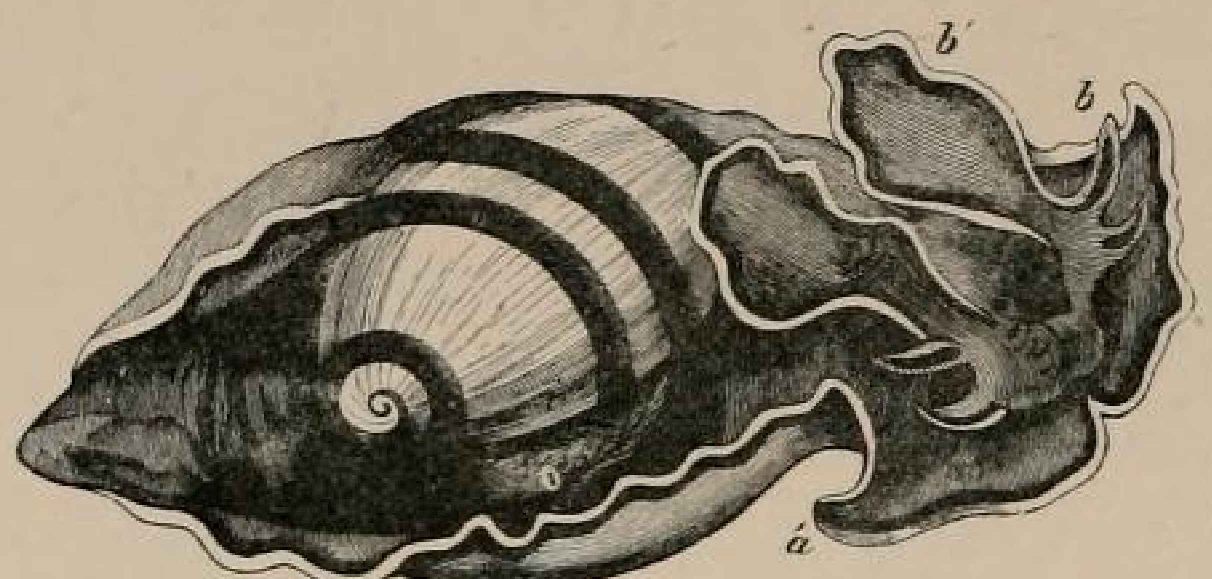


FIG. 52.—*Bulla vexillum* (Chemnitz), as seen crawling. *á*, oral hood (compare with Tethys, fig. 62, B), possibly a continuation of the epipodia; *b*, *b′*, cephalic tentacles. (From Owen.)

FIG. 53.—Tornatella. *h*, shell; *b*, oral hood; *d*, foot; *f*, operculum.

The Euthyneura comprise two orders, the Opisthobranchia and the Pulmonata.

Order 1.—**Opisthobranchia.**

Marine Euthyneura the more archaic forms of which have a relatively large foot and a small visceral hump, from the base of which projects on the right side a short mantle-skirt. The anus is placed in such forms far back beyond the mantle-skirt. In front of the anus, and only partially covered by the mantle-skirt, is the ctenidium with its free end turned backwards. The heart lies in front of, instead of to the side of, the attachment of the ctenidium, —hence Opisthobranchia as opposed to "Prosobranchia," which correspond to the Streptoneura. A shell is possessed in the adult state by but few Opisthobranchia, but all pass through a veliger larval stage with a nautiloid shell (fig. 60). Many Opisthobranchia have by a process of atrophy lost the typical ctenidium and the mantle-skirt, and have developed other organs in their place. As in some Azygobranchia, the free margin of the mantle-skirt is frequently reflected over the shell when a shell exists; and, as in some Azygobranchia, broad lateral outgrowths of the foot (epipodia) are often developed, which, as does *not* occur in Azygobranchia, may be thrown over the shell or naked dorsal surface of the body.

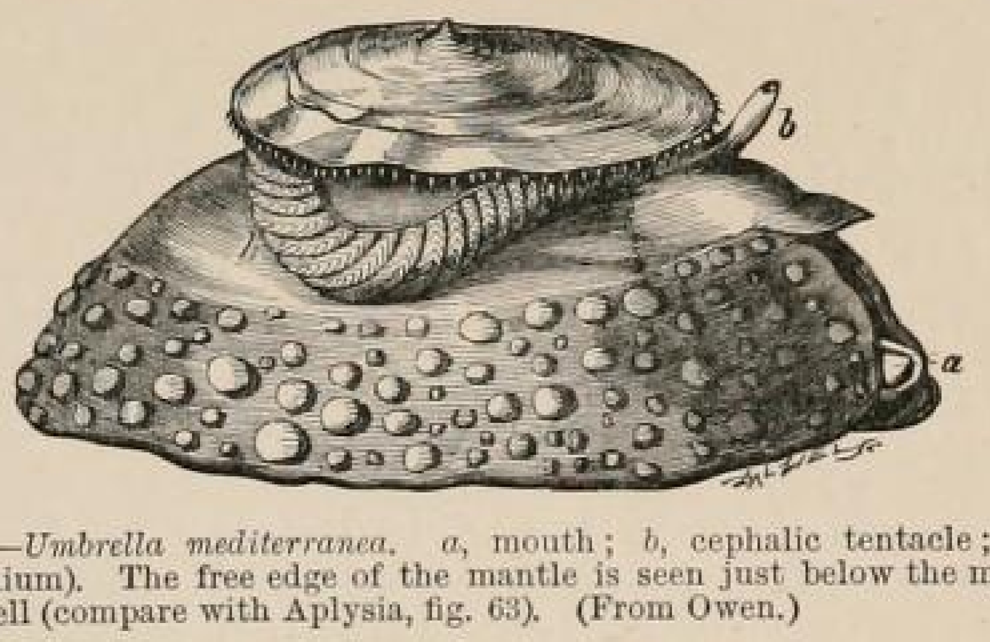


FIG. 54.—*Umbrella mediterranea*. *a*, mouth; *b*, cephalic tentacle; *h*, gill (ctenidium). The free edge of the mantle is seen just below the margin of the shell (compare with Aplysia, fig. 63). (From Owen.)

The variety of special developments of structure accompanying the atrophy of typical organs in the Opisthobranchia and general degeneration of organization is very great, and renders their classification difficult. Two sections of the order may be distinguished, according as the typical Molluscan mantle-skirt (limbus pallialis) is or is not atrophied, and within each section certain sub-orders.

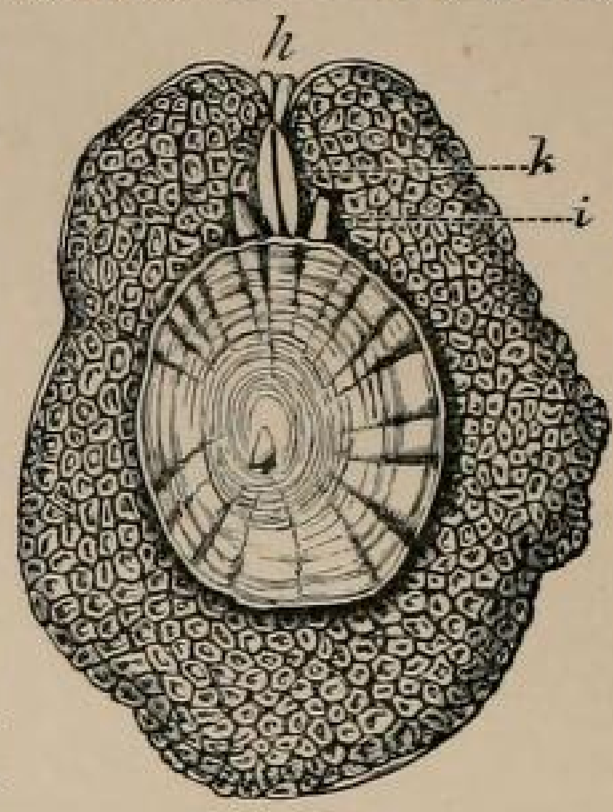


FIG. 55.—*Umbrella mediterranea*, seen from above. *h*, mouth; *i*, cephalic tentacles; *k*, penis-sheath. (After Keferstein.)

Section *a*.—*PALLIATA* (= *Tectibranchiata*, Woodward)—the typical Molluscan mantle-skirt or pallium retained.

Sub-order 1.—*Ctenidiobranchia.*

Characters.—Palliata in which the ctenidium is retained as the branchial organ; with rare exceptions a delicate shell, which may be very small or completely enclosed by the reflected margin of the mantle; epipodia (lateral outgrowths of the foot) frequently present.

Family 1.—*Tornatellidæ.*
Genera: *Tornatella*, Lam. (fig. 53); *Cinulia*, Gray, &c.
Family 2.—*Bullidæ.*
Genera: *Bulla*, Lam. (fig. 52); *Acera*, Müller; *Scaphander*, Montf.; *Bullæa*, Lam.; *Doridium*, Meckel; *Gastropteron*, Meckel, &c.
Family 3.—*Aplysiidæ.*
Genera: *Aplysia*, Gmelin (the Sea-Hare) (figs. 20, 56, &c.); *Dolobella*, Lam.; *Lobiger*, Krohn, &c.
Family 4.—*Pleurobranchidæ.*
Genera: *Pleurobranchus*, Cuvier; *Umbrella*, Chemnitz (figs. 54, 55); *Runcina*, Forbes, &c.

Sub-order 2.—*Phyllidiobranchia.*

Characters.—Palliata in which the ctenidia have atrophied; much as in Patellidæ among the Zygobranchiate Streptoneura their place is taken by laterally-placed lamellæ, developed from the inner surface of the bilaterally-disposed mantle-skirt in two lateral rows.

Family 5.—*Phyllidiadæ.*
Genera: *Phyllidia*, Cuiver; *Pleurophyllidia*, Meck. (fig. 57).

Section *b*.—*NON-PALLIATA.*

Characters.—The typical Molluscan mantle-skirt is atrophied in the adult. No shell is present in the adult, though the dorsal integument may be strengthened by calcareous spicules (Doris). The otocysts are not sessile on the pedal ganglia as in other Gastropods, but, as in the Natantia Azygobranchia, lie close to the cerebral ganglia. In one sub-order (Pygobranchia) the typical ctenidium appears to be retained in a modified form; in the others special developments of the body-wall take its place, or no special respiratory processes exist at all. The general form of the body is slug-like, the foot and visceral hump being coextensive, and a secondary bilateral symmetry is asserted by the usually median (sometimes right-sided) dorsal position of the anus on the hinder part of the body.

Sub-order 1.—*Pygobranchia.*

Characters.—The ctenidium assumes the form of a circlet of pinnate processes surrounding the median dorsal anus; a strongly-marked epipodial fold may occur all round the foot and simulate a mantle-skirt (see fig. 62, C, Doris); papillæ or "cerata" of the dorsal integument may occur as well as the true ctenidium (fig. 61).

Family 6.—*Dorididæ.*
Genera: *Doris*, L.; *Goniodoris*, Forbes; *Triopa*, Johnst.; *Ægirus*, Loven; *Thecacera*, Fleming; *Polycera*, Cuvier; *Idalia*, Leuckart; *Ancula*, Loven; *Ceratosoma*, Adams; *Onchidoris*, Blainv.

Sub-order 2.—*Ceratonota.*

Characters.—The typical Molluscan ctenidium is not developed; upon the dorsal area is developed a more or less numerous series of cylindrical or branched processes (the cerata) into each of which the intestine usually sends a process; anus dorsal, median, or right-sided.

Family 7.—*Tritoniadæ.*
Genera: *Tritonia*, Cuvier; *Scyllæa*, L.; *Tethys*, L. (fig. 62, B); *Dendronotus*, A. and H.; *Doto*, Oken.
Family 8.—*Eolidæ.*
Genera: *Eolis*, Cuvier (fig. 62, A); *Glaucus*, Forster; *Fiona*, A. and H. (fig. 67); *Embletonia*, A. and H.; *Proctonotus*, A. and H.; *Antiopa*, A. and H.; *Hermæa*, Loven; *Alderia*, Allman.

Sub-order 3.—*Haplomorpha.*

Characters.—No ctenidia, cerata, mantle-skirt, or other processes of the body-wall; degenerate forms of small size.

Family 9.—*Phyllirhoidæ.*
Genera: *Phyllirhoë*, Peron and Lesueur (fig. 58); *Acura*, Adams.
Family 10.—*Elysiadæ.*
Genera: *Elysia*, Risso (fig. 62, D, E); *Acteonia*, Quatref.; *Cenia*, A. and H.; *Limapontia*, Johnston; *Rhodope*, Köll.

Further Remarks on the Opisthobranchia.—The Opisthobranchia present the same wide range of superficial appearance as do the Azygobranchiate Streptoneura, forms carrying well-developed spiral shells and large mantle-skirts being included in the group, together with flattened or cylindrical slug-like forms. But in respect of the substitution of other parts for the mantle-skirt and for the gill which the more degenerate Opisthobranchia exhibit, this Order stands alone. Some Opisthobranchia are striking examples of degeneration (some Haplomorpha), having none of those regions or processes of the body developed which distinguish the archaic Mollusca from such flat-worms as the Dendrocœl Planarians. Indeed, were it not for their retention of the characteristic odontophore we should have little or no indication that such forms as Phyllirhoë and Limapontia really belong to the Mollusca at all. The interesting little *Rhodope Veranyii*, which has no odontophore, has been associated by systematists both with these simplified Opisthobranchs and with Rhabdocœl Planarians (**29**).

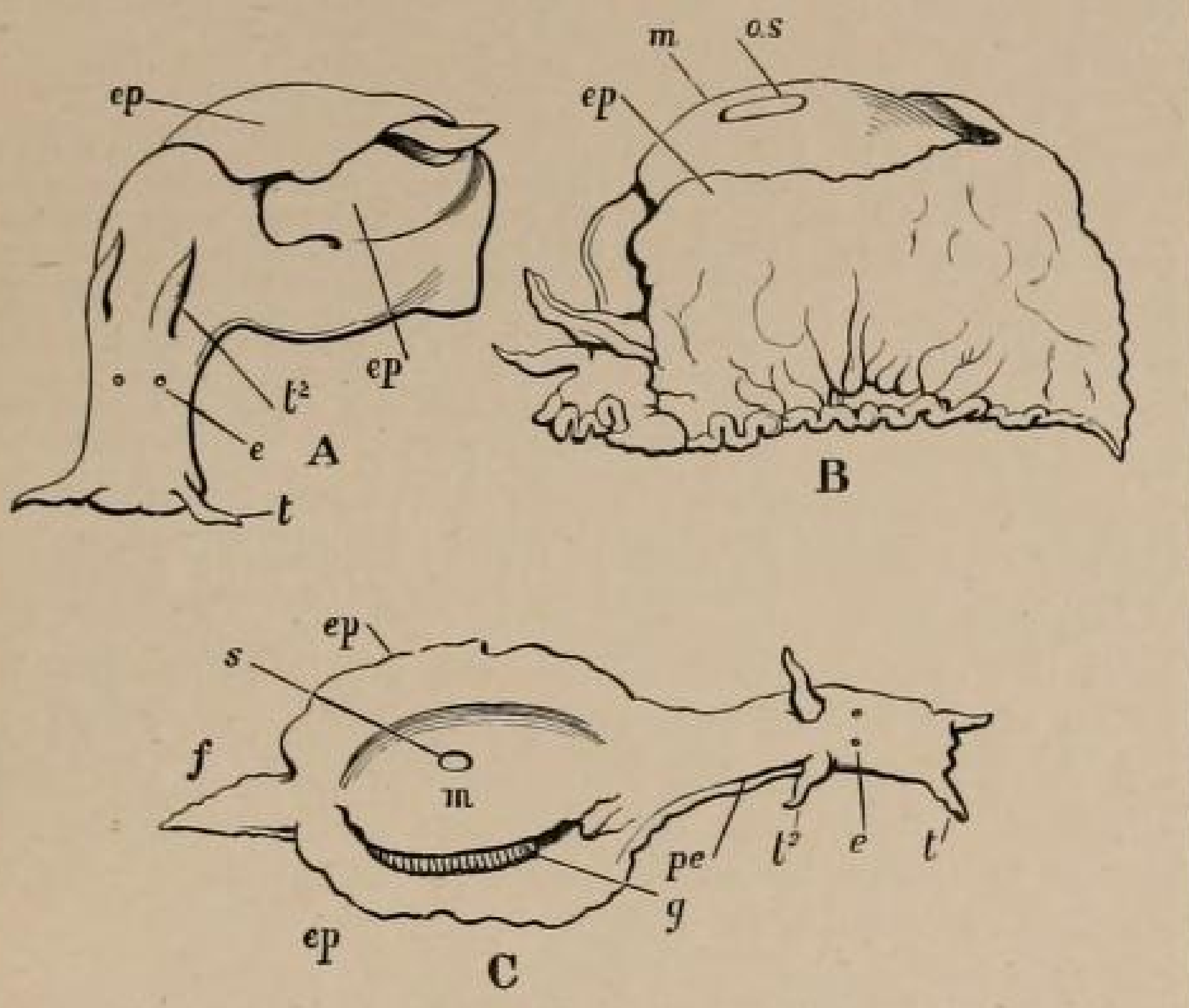


FIG. 56.—Three views of Aplysia sp., in various conditions of expansion and retraction. *t*, anterior cephalic tentacles; *t*², posterior cephalic tentacles; *e*, eyes; *f*, metapodium; *ep*, epipodium; *g*, gill-plume (ctenidium); *m*, mantle-flap reflected over the thin oval shell; *os*, *s*, orifice formed by the unclosed border of the reflected mantle-skirt, allowing the shell to show; *pe*, the spermatic groove. (After Cuvier.)

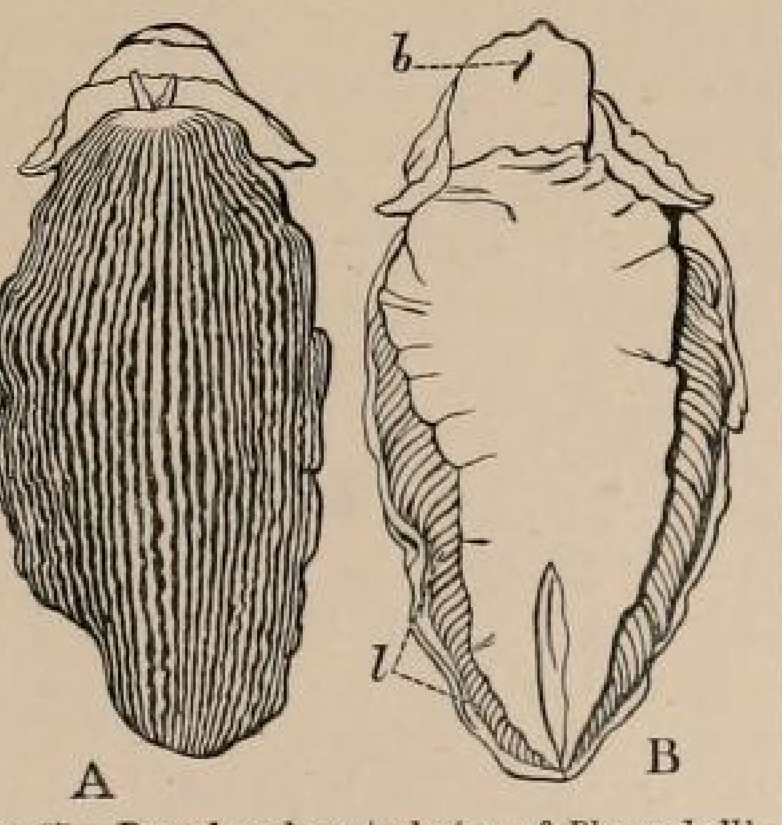


FIG. 57.—Dorsal and ventral view of *Pleurophyllidia lineata* (Otto), one of the Phyllidiobranchiate Palliate Opisthobranchs. *b*, the mouth; *l*, the lamelliform sub-pallial gills, which (as in Patella) replace the typical Molluscan ctenidium. (After Keferstein.)

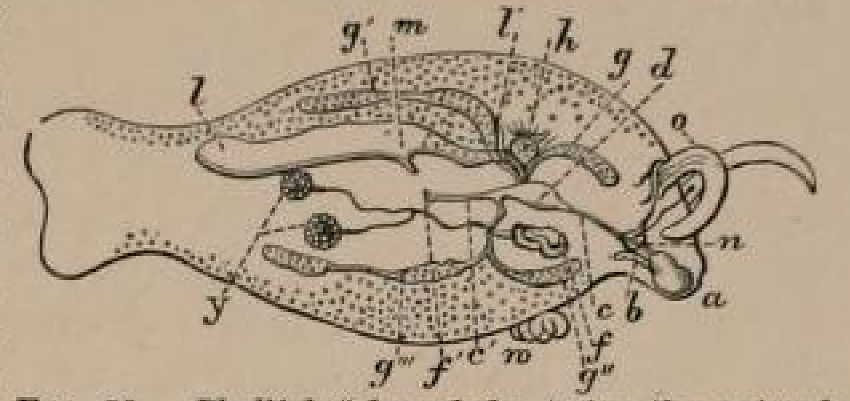


FIG. 58.—*Phyllirhoë bucephala*, twice the natural size, a transparent pisciform pelagic Opisthobranch. The internal organs are shown as seen by transmitted light. *a*, mouth; *b*, radular sac; *c*, œsophagus; *d*, stomach; *c'*, intestine; *f'*, anus; *g*, *g'*, *g''*, *g'''*, the four lobes of the liver; *h*, the heart (auricle and ventricle); *l*, the renal sac (nephridium); *l'*, the ciliated communication of the renal sac with the pericardium; *m*, the external opening of the renal sac; *n*, the cerebral ganglion; *o*, the cephalic tentacles; *f*, the genital pore; *y*, the ovo-testes; *w*, the parasitic hydromedusa *Mnestra*, usually found attached in this position by the aboral pole of its umbrella. (After Keferstein.)

In many respects the Sea-Hare (Aplysia) of which several species are known (some occurring on the English coast), serves as a convenient example of the fullest development of the organization characteristic of Opisthobranchia. The woodcut (fig. 56) gives a faithful representation of the great mobility of the various parts of the body. The head is well marked and joined to the body by a somewhat constricted neck. It carries two pairs of cephalic tentacles and a pair of sessile eyes. The visceral hump is low and not drawn out into a spire. The foot is long, carrying the oblong visceral mass upon it, and projecting (as metapodium) a little beyond it (*f*). Laterally the foot gives rise to a pair of mobile fleshy lobes, the epipodia (*ep*), which can be thrown up so as to cover in the dorsal surface of the animal. Such epipodia are common, though by no means universal, among Opisthobranchia. The torsion of the visceral hump is not carried out very fully, the consequence being that the anus has a posterior position a little to the right of the median line above the metapodium, whilst the branchial chamber formed by the overhanging mantle-skirt faces the right side of the body instead of lying well to the front as in Streptoneura and as in Pulmonate Euthyneura. The gill-plume which in Aplysia is the typical Molluscan ctenidium is seen in fig.

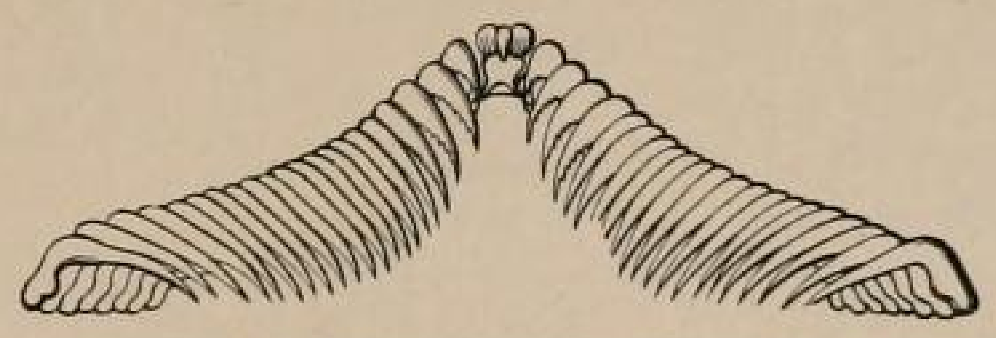


FIG. 59.—*Acera bullata.* A single row of teeth of the radula. (Formula, x.1.x.)

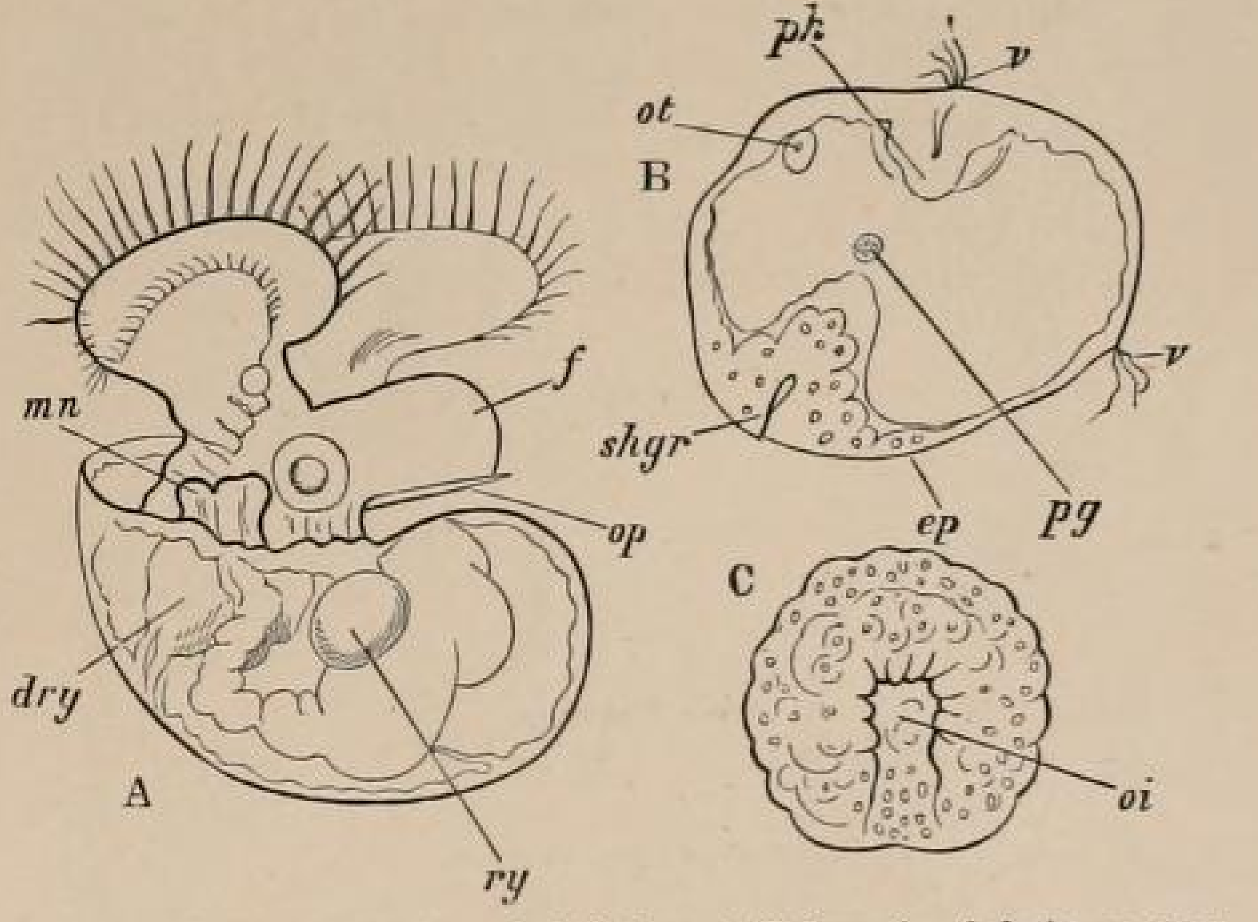


FIG. 60.—A. Veliger-larva of an Opisthobranch (Polycera). *f*, foot; *op*, operculum; *mn*, anal papilla; *ry*, *dry*, two portions of unabsorbed nutritive yelk on either side the intestine. The right otocyst is seen at the root of the foot. B. Trochosphere of an Opisthobranch (Pleurobranchidium) showing: *shgr*, the shell-gland or primitive shell-sac; *v*, the cilia of the velum; *ph*, the commencing stomodæum or oral invagination; *ot*, the left otocyst; *pg*, red-coloured pigment spot. C. Diblastula of an Opisthobranch (Polycera) with elongated blastopore *oi*. (All from Lankester.)

63 projecting from the branchial sub-pallial space. The relation of the delicate shell to the mantle is peculiar, since it occupies an oval area upon the visceral hump, the extent of which is indicated in fig. 56, C, but may be better understood by a glance at the figures of the allied genus Umbrella (figs. 54, 55), in which the margin of the mantle-skirt coincides, just as it does in the Limpet, with the margin of the shell. But in Aplysia the mantle is reflected over the edge of the shell, and grows over its upper surface so as to completely enclose it, excepting at the small central area *s* where the naked shell is exposed. This enclosure of the shell is a permanent development of the arrangement seen in many Streptoneura (*e.g.*, Pyrula, Ovulum, see figs. 38 and 41), where the border of the mantle can be, and usually is, drawn over the shell, though it is withdrawn (as it cannot be in Aplysia) when they are irritated. From the fact that Aplysia commences its life as a free-swimming Veliger with a nautiloid shell not enclosed in any way by the border of the mantle, it is clear that the enclosure of the shell in the adult is a secondary process. Accordingly, the shell of Aplysia must not be confounded with a primitive shell in its shell-sac, such as we find realized in the shells of Chiton and in the plugs which form in the remarkable transitory "shell-sac" or "shell-gland" of Molluscan embryos (see figs. 7, 68, and 72***). Aplysia, like other Mollusca, develops a primitive shell-sac in its trochosphere stage of development (fig. 68), which disappears and is succeeded by a nautiloid shell (fig. 60). This forms the nucleus of the adult shell, and, as the animal grows, becomes enclosed by a reflexion of the mantle-skirt. In reference to the possible comparison of the enclosed shell of Aplysia and its allies with those of some Slugs and of Cuttle-fishes, the reader is referred to the paragraphs dealing especially with those Molluscs. When the shell of an Aplysia enclosed in its mantle is pushed well to the left, the sub-pallial space is fully exposed as in fig. 63, and the various apertures of the body are seen. Posteriorly we have the anus, in front of this the lobate gill-plume, between the two (hence corresponding in position to that of the Azygobranchia) we have the aperture of the renal organ. In front, near the anterior attachment of the gill-plume, is the osphradium (olfactory organ) discovered by Spengel, yellowish in colour, in the typical position, and overlying an olfactory ganglion with typical nerve-connexion (see fig. 20). To the right of Spengel's osphradium is the opening of a peculiar gland which has, when dissected out, the form of a bunch of grapes; its secretion is said to be poisonous. On the under side of the free edge of the mantle are situated the numerous small cutaneous glands which, in the large *Aplysia camelus* (not in other species), form the purple secretion which was known to the ancients. In front of the osphradium is the single genital pore, the aperture of the common or hermaphrodite duct. From this point there stretches forward to the right side of the head a groove—the spermatic groove—down which the spermatic fluid passes. In other Euthyneura this groove may close up and form a canal. At its termination by the side of the head is the muscular introverted penis. In the hinder part of the foot (not shown in any of the diagrams) is the opening of a large mucous-forming gland very often found in the Molluscan foot.

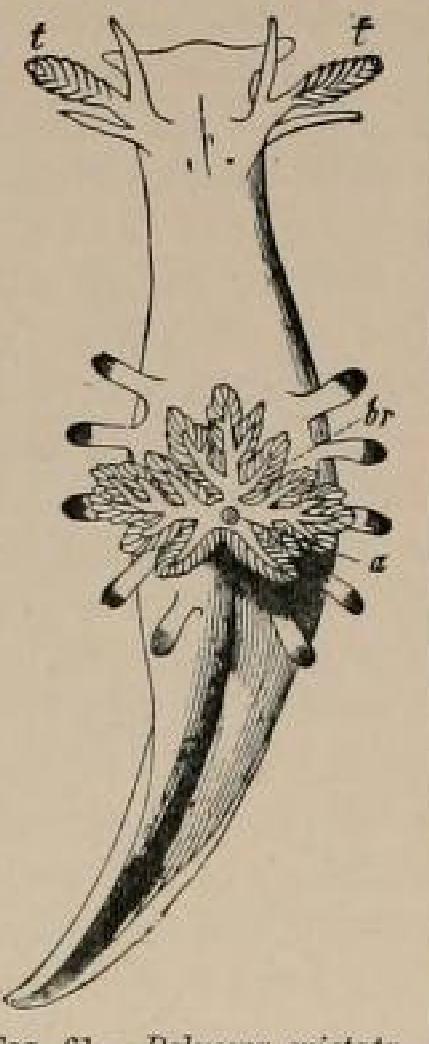


Fig. 61.—*Polycera cristata*, one of the Pygobranchiate Opisthobranchs (dorsal view). *a*, anus; *br*, the ctenidium peculiarly modified so as to encircle the anus; *t*, cephalic tentacles. External to the branchial ctenidium are seen ten club-like processes of the dorsal wall, these are the "cerata" which are characteristically developed in another sub-order of Opisthobranchs, the Ceratonota (see fig. 62, A). (From Gegenbaur, after Alder and Hancock.)

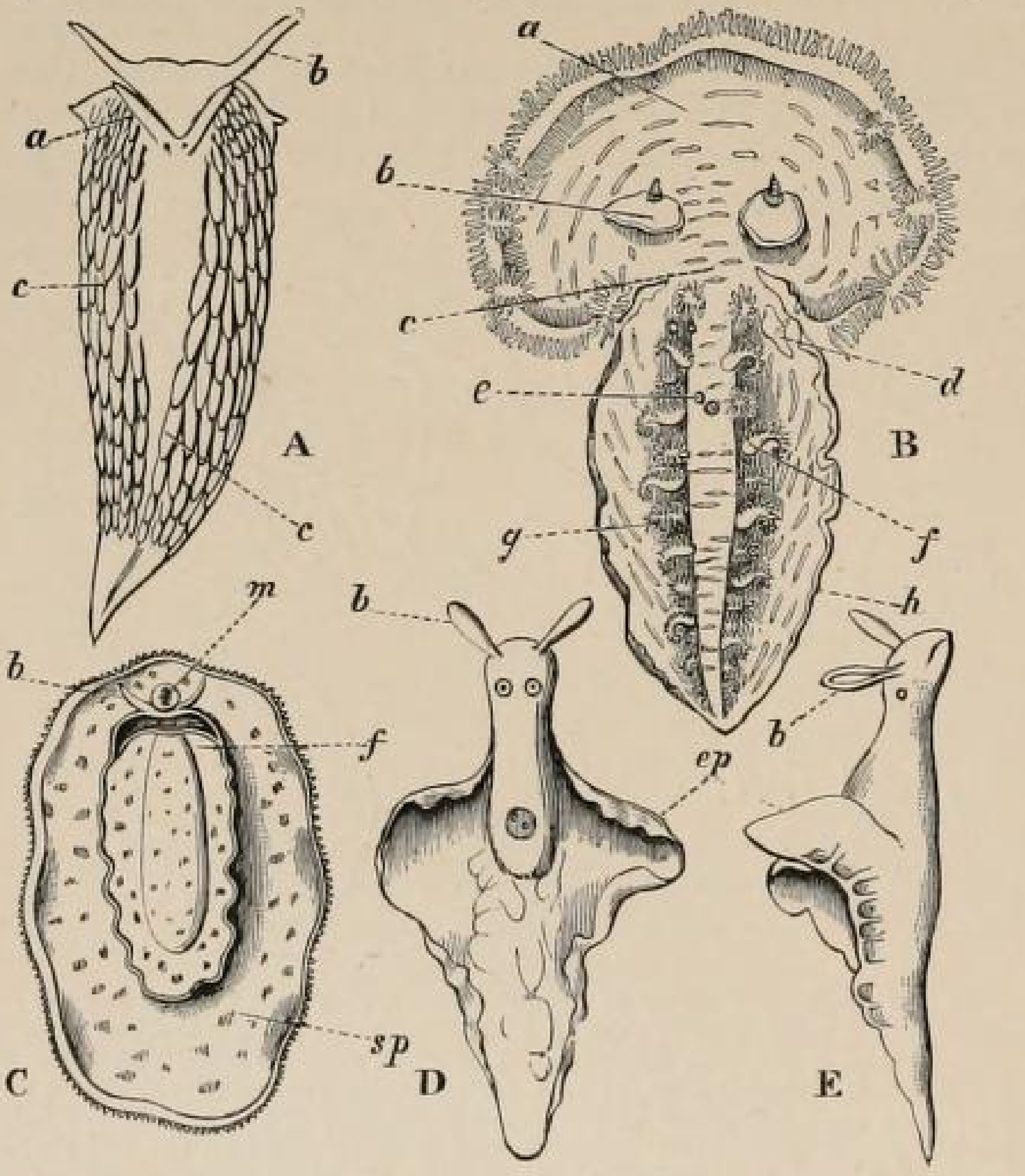


Fig. 62.

A. *Eolis papillosa* (Lin.), dorsal view. *a*, *b*, posterior and anterior cephalic tentacles; *c*, the dorsal "cerata" (hence Ceratobranchia).

B. *Tethys leporina*, dorsal view. *a*, the cephalic hood; *b*, cephalic tentacles; *c*, neck; *d*, genital pore; *e*, anus; *f*, large cerata; *g*, smaller cerata; *h*, margin of the foot.

C. *Doris* (*Actinocyclus*) *tuberculatus* (Cuv.), seen from the pedal surface. *m*, mouth; *b*, margin of the head; *f*, sole of the foot; *sp*, the mantle-like epipodium.

D, E. Dorsal and lateral view of *Elysia* (*Actæon*) *viridis*. *ep*, epipodial outgrowths. (After Keferstein.)

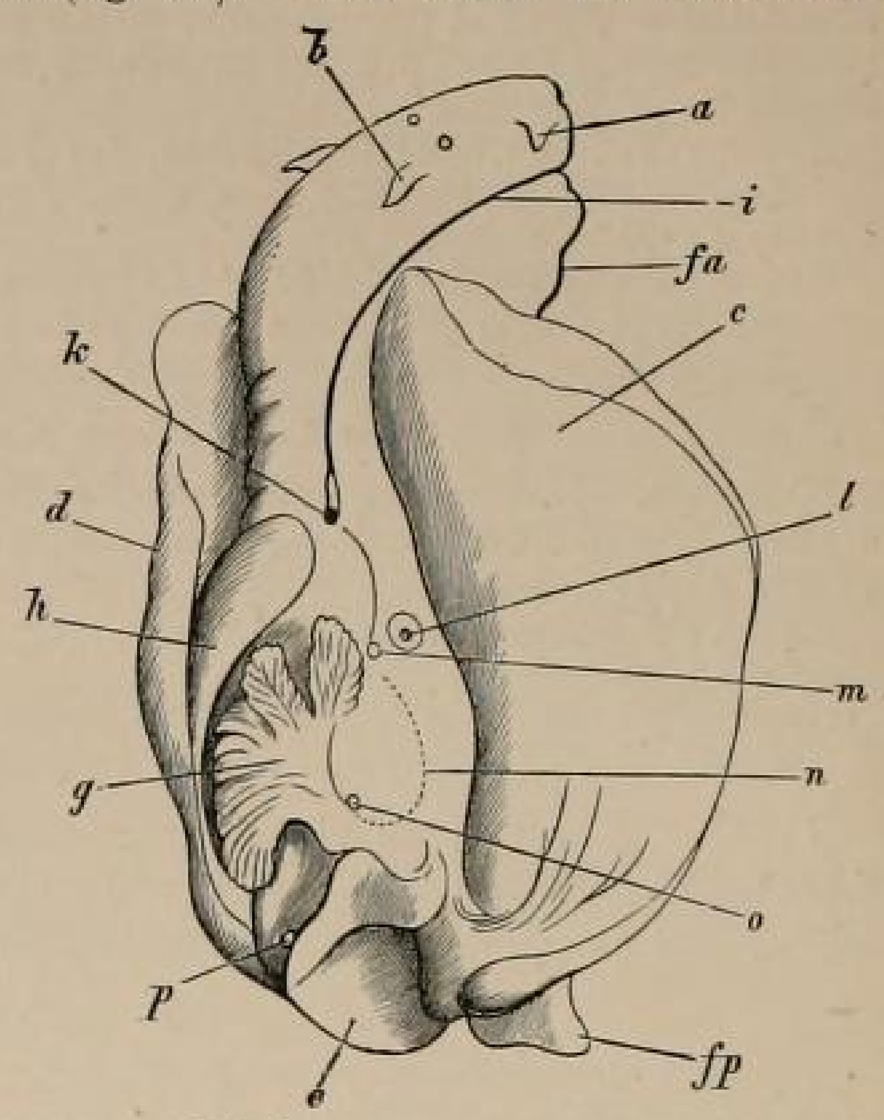


Fig. 63.—*Aplysia leporina* (*camelus*, Cuv.), with epipodia and mantle reflected away from the mid-line. *a*, anterior cephalic tentacle; *b*, posterior do.; between *a* and *b*, the eyes; *c*, right epipodium; *d*, left epipodium; *e*, hinder part of visceral hump; *fp*, posterior extremity of the foot; *fa*, anterior part of the foot underlying the head; *g*, the ctenidium (branchial plume); *h*, the mantle-skirt tightly spread over the horny shell and pushed with it towards the left side; *i*, the spermatic groove; *k*, the common genital pore (male and female); *l*, orifice of the grape-shaped (supposed poisonous) gland; *m*, the osphradium (olfactory organ of Spengel); *n*, outline of part of the renal sac (nephridium) below the surface; *o*, external aperture of the nephridium; *p*, anus. (Original.)

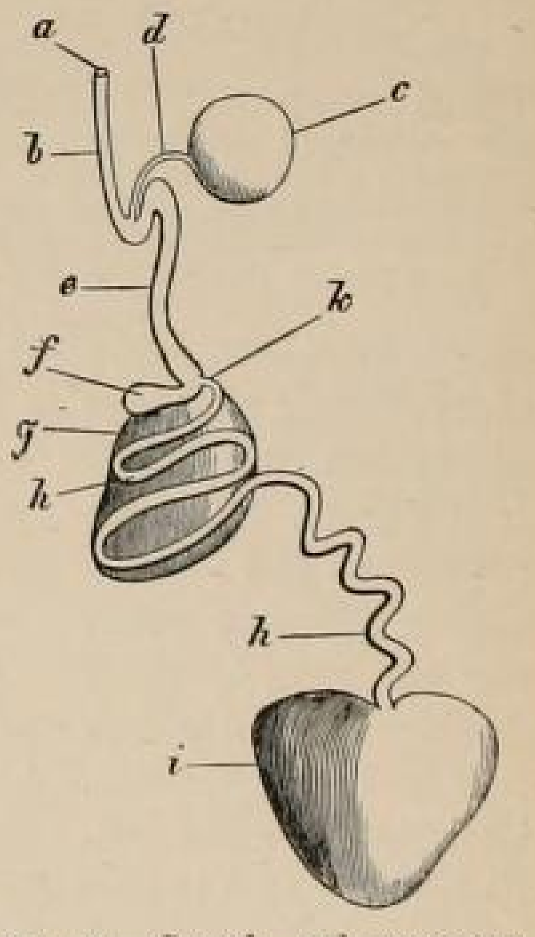


Fig. 64.—Gonad, and accessory glands and ducts of Aplysia. *i*, ovo-testis; *h*, hermaphrodite duct; *g*, albuminiparous gland; *f*, vesicula seminalis; *k*, opening of the albuminiparous gland into the hermaphrodite duct; *e*, hermaphrodite duct (uterine portion); *b*, vaginal portion of the uterine duct; *c*, spermatheca; *d*, its duct; *a*, genital pore. (Original.)

With regard to internal organization we may commence with the disposition of the renal organ (nephridium), the external opening of which has already been noted. The position of this opening and other features of the renal organ have been determined recently by Mr. J. T. Cunningham, Fellow of University College, Oxford, who writes as follows from Naples, February 1883 :—

> "There is considerable uncertainty with respect to the names of the species of Aplysia. There are two forms which are very common in the Gulf of Naples, and which I have used in studying the anatomy of the renal organ in the genus. One is quite black in colour, and measures when outstretched eight or nine inches in length. The other is light brown and somewhat smaller, its length usually not exceeding seven inches. The first is flaccid and sluggish in its movements, and has not much power of contraction ; its epipodial lobes are enormously developed and extend far forward along the body ; it gives out when handled an abundance of purple liquid, which is derived from cutaneous glands situated on the under side of the free edge of the mantle. In the Zoological Station this form is known as *Ap. leporina* ; but according to Blochmann it is identical with *A. Camelus* of Cuvier. The other species is *A. depilans* ; it is firm to the touch, and contracts forcibly when irritated ; the secretion of the mantle-glands is not abundant, and is milky white in appearance. The kidney has similar relations in both genera, and is identical with the organ spoken of by many authors as the triangular gland. Its superficial extent is seen when the folds covering the shell are cut away and the shell removed ; the external surface forms a triangle with its base bordering the pericardium and its apex directed posteriorly and reaching to the left-hand posterior corner of the shell-chamber. The dorsal surface of the kidney extends to the left beyond the shell-chamber beneath the skin in the space between the shell-chamber and the left epipodium.
>
> "When the animal is turned on its left-hand side and the mantle-chamber widely opened, the gill being turned over to the left, a part of the kidney is seen beneath the skin between the attachment of the gill and the right epipodium (fig. 63). On examination this is found to be the under surface of the posterior limb of the gland, the upper surface of which has just been described as lying beneath the shell. In the posterior third of this portion, close to that edge which is adjacent to the base of the gill, is the external opening (fig. 63, *o*).
>
> "When the pericardium is cut open from above in an animal otherwise entire, the anterior face of the kidney is seen forming the posterior wall of the pericardial chamber ; on the deep edge of this face, a little to the left of the attachment of the auricle to the floor of the pericardium, is seen a depression ; this depression contains the opening from the pericardium into the kidney.
>
> "To complete the account of the relations of the organ : the right anterior corner can be seen superficially in the wall of the mantle-chamber above the gill. Thus the base of the gill passes in a slanting direction across the right-hand side of the kidney, the posterior end being dorsal to the apex of the gland, and the anterior end ventral to the right-hand corner.
>
> "As so great a part of the whole surface of the kidney lies adjacent to external surfaces of the body, the remaining part which faces the internal organs is small ; it consists of the left part of the under surface ; it is level with the floor of the pericardium, and lies over the globular mass formed by the liver and convoluted intestine.
>
> "Mere dissection does not give sufficient evidence concerning such communications as these of the kidney in Aplysia. I studied the external opening by taking a series of sections through the surrounding region of the gland ; to demonstrate the internal aperture injected a solution of Berlin blue into the pericardium ; it did not fill the whole kidney easily, but ran down into the part adjacent to the base of the gill."

Thus the renal organ of Aplysia is shown to conform to the Molluscan type. The heart lying within the adjacent pericardium has the usual form, a single auricle and ventricle. The vascular system is not extensive, the arteries soon ending in the well-marked spongy tissue which builds up the muscular foot, epipodia, and dorsal body-wall.

The alimentary canal commences with the usual buccal mass ; the lips are cartilaginous, but not armed with horny jaws, though these are common in other Opisthobranchs ; the lingual ribbon is multidenticulate, and a pair of salivary glands pour in their secretion. The œsophagus expands into a curious gizzard, which is armed internally with large horny processes, some broad and thick, others spinous, fitted to act as crushing instruments. From this we pass to a stomach and a coil of intestine embedded in the lobes of a voluminous liver ; a cæcum of large size is given off near the commencement of the intestine. The liver opens by two ducts into the digestive tract.

The generative organs lie close to the coil of intestine and liver, a little to the left side. When dissected out they appear as represented in fig. 64. The essential reproductive organ or gonad consists of both ovarian and testicular cells (see fig. 65). It is an ovo-testis. From it passes a common or hermaphrodite duct, which very soon becomes entwined in the spire of a gland—the albuminiparous gland. The latter opens into the common duct at the point *x*, and here also is a small diverticulum of the duct *y*. Passing on, we find not far from the genital pore a glandular spherical body (the spermatheca *a*) opening by means of a longish duct into the common duct, and then we reach the pore (fig. 63, *k*). Here the female apparatus terminates. But when the male secretion of the ovo-testis is active, the seminal fluid passes from the genital pore along the spermatic groove (fig. 63,) to the penis, and is by the aid of that eversible muscular organ introduced into the genital pore of a second Aplysia, whence it passes into the spermatheca, there to await the activity of the female element of the ovo-testis of this second Aplysia. After an interval of some days—possibly weeks—the ova of the second Aplysia commence to descend the hermaphrodite duct ; they become enclosed in a viscid secretion at the point where the albuminiparous gland opens into the duct intertwined with it ; and on reaching the point where the spermathecal duct debouches they are impregnated by the spermatozoa which escape now from the spermatheca and meet the ova.

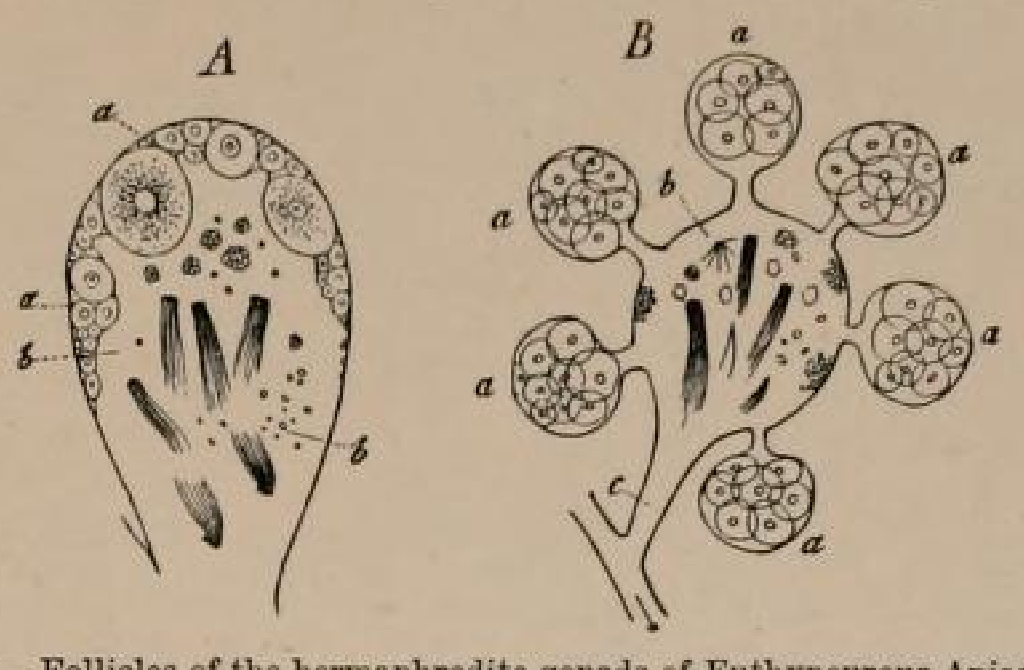


Fig. 65.—Follicles of the hermaphrodite gonads of Euthyneurous Anisopleura. —*A*, of Helix ; *B*, of Eolidia. *a*, ova ; *b*, developing spermatozoids ; *c*, common efferent duct.

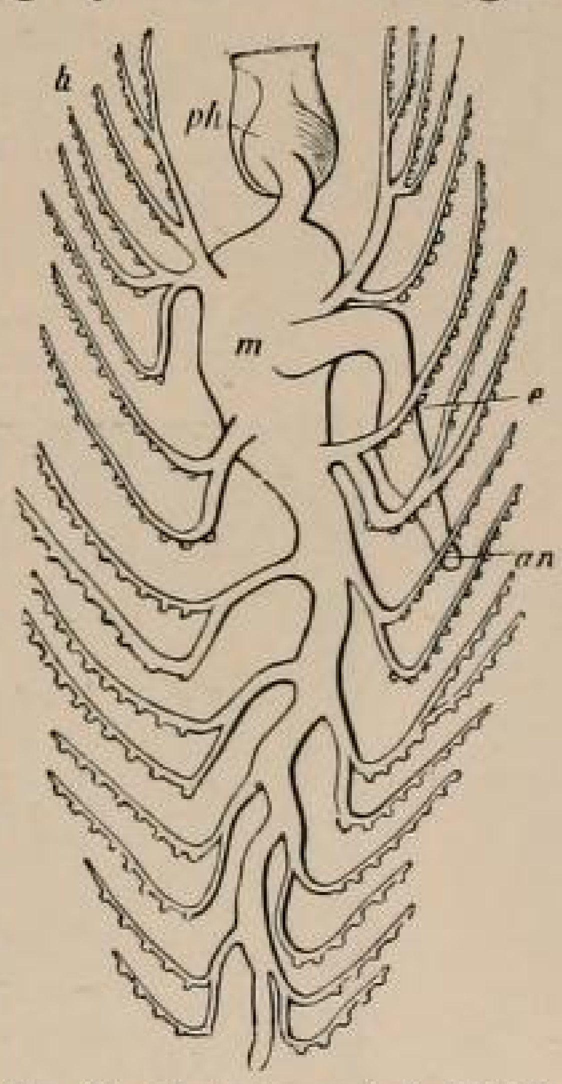


Fig. 66. Enteric canal of *Æolidia papillosa*. *ph*, pharynx ; *m*, mid-gut, with its hepatic appendages *h*, all of which are not figured ; *e*, hind gut ; *an*, anus. (From Gegenbaur, after Alder and Hancock.)

The development of Aplysia from the egg presents many points of interest from the point of view of comparative embryology, but in relation to the morphology of the Opisthobranchia it is sufficient to point to the occurrence of a trochosphere and a veliger stage (fig. 60), and of a shell-gland or primitive shell-sac (fig. 68, *shs*), which is succeeded by a nautiloid shell.

The nervous system of Aplysia will be found on comparison of fig. 20, which represents it, with our schematic Mollusc (fig. 1, D) to present but little modification. It is in fact a nervous system in which the great ganglion-pairs are well developed and distinct. The Euthyneurous visceral loop is long, and presents only one ganglion (in *Aplysia camelus*, but two distinct ganglia joined to one another in

Aplysia hybrida of the English coast), placed at its extreme limit, representing both the right and left visceral ganglia and the third or abdominal ganglion, which are so often separately present. The diagram (fig. 20) shows the nerve connecting this abdomino-visceral ganglion with the olfactory ganglion of Spengel. It is also seen to be connected with a more remote ganglion—the genital. Such special irregularities in the development of ganglia upon the visceral loop, and on one or more of the main nerves connected with it, are, as the figures of Molluscan nervous systems given in this article show, very frequent. Our figure of the nervous system of Aplysia does not give the small pair of buccal ganglia which are, as in all Glossophorous Molluscs, present upon the nerves passing from the cerebral region to the odontophore.

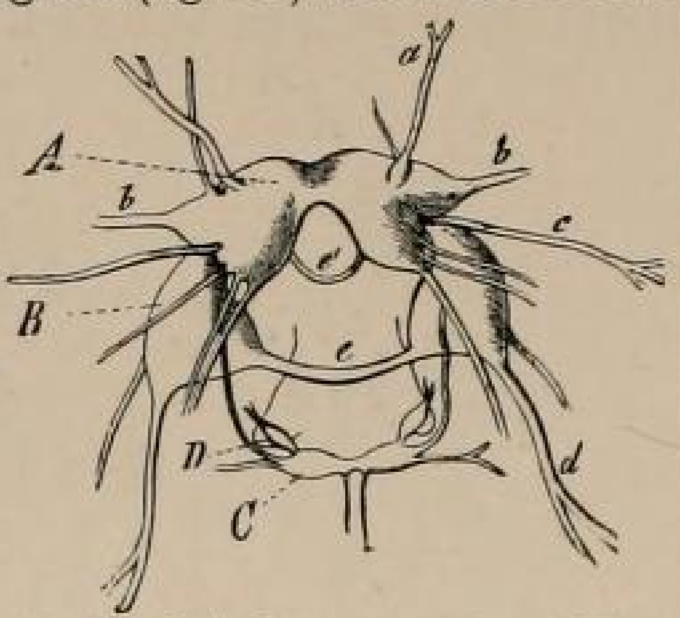


Fig. 67.—Central nervous system of Fiona (one of the Ceratonotous Opisthobranchs), showing a tendency to fusion of the great ganglia. *A*, cerebral, pleural, and visceral ganglia united; *B*, pedal ganglion; *C*, buccal ganglion; *D*, œsophageal ganglion connected with the buccal; *a*, nerve to superior cephalic tentacle; *b*, nerves to inferior cephalic tentacles; *c*, nerve to generative organs; *d*, pedal nerve; *e*, pedal commissure; *e'*, visceral loop or commissure (?). (From Gegenbaur, after Bergh.)

For a comparison of various Opisthobranchs, Aplysia will be found to present a convenient starting-point. It is one of the more typical Opisthobranchs, that is to say, it belongs to the section Palliata, but other members of the Palliata, namely, Bulla and Tornatella (figs. 52 and 53), are less abnormal than Aplysia in regard to their shells and the form of the visceral hump. They have naked spirally-twisted shells which may be concealed from view in the living animal by the expansion and reflexion of the epipodia, but are not enclosed by the mantle, whilst Tornatella is remarkable amongst all Euthyneura for possessing an operculum like that of so many Streptoneura.

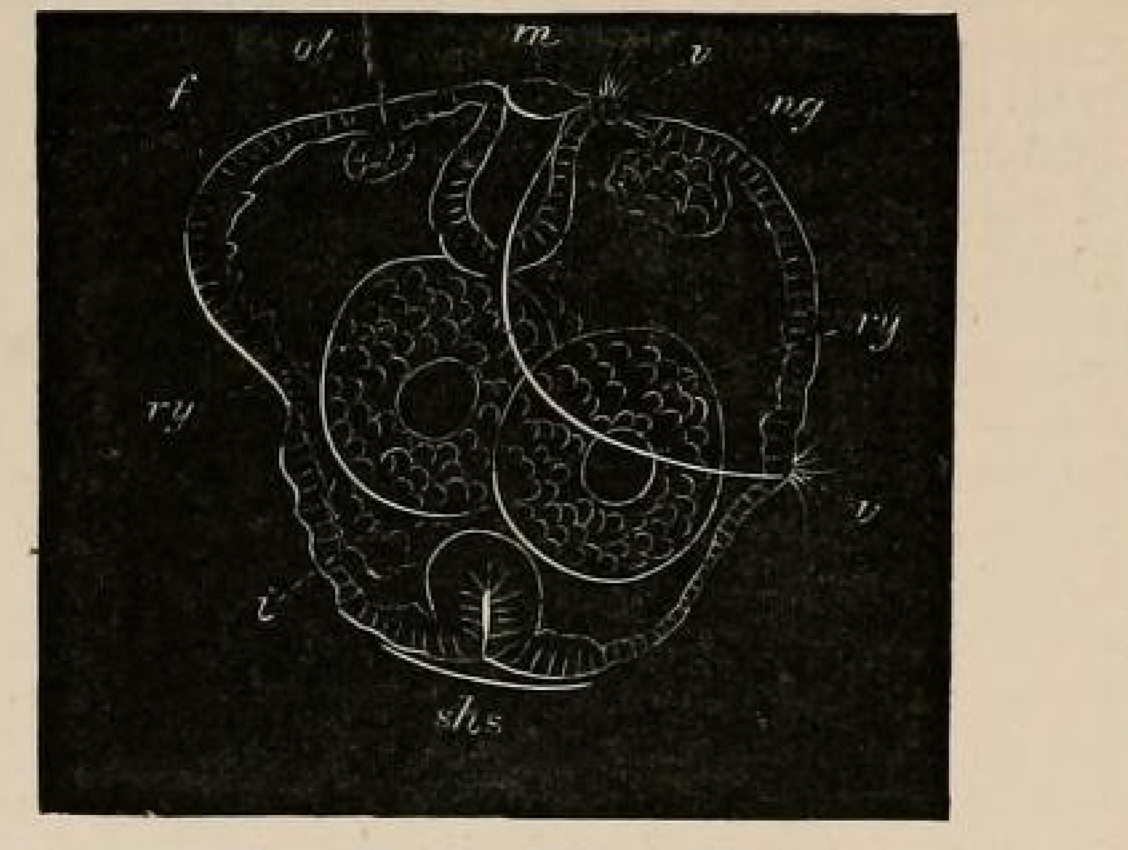


Fig. 68.—Young veliger larva of an Opisthobranch (Pleuro-branchidium). *m*, mouth; *v*, ciliated band marking off the velum; *ng*, cerebral ganglion developing from epiblast, within the velar area; *ot*, otocyst also developing from epiblast; *f*, foot; *i*, intestine; *ry*, residual nutritive yelk; *shs*, primitive shell-sac or shell-gland. (From Lankester.)

The great development of the epipodia seen in Aplysia is usual in Palliate Opisthobranchs; it occurs also in Elysia (fig. 62, D) among Non-Palliata; in Doris it seems probable that the mantle-like fold overhanging the foot is to be interpreted as epipodium, the mantle-skirt being altogether absent, as shown by the naked position of the gills and anus on the dorsal surface (figs. 61 and 62, C). The whole surface of the body becomes greatly modified in those Non-Palliate forms which have lost, not only the mantle-skirt and the shell, but also the ctenidium. Many of these (Ceratonota) have peculiar processes developed on the dorsal surface (fig. 62, A, B), or retain purely negative characters (fig. 62, D). The chief modification of internal organization presented by these forms, as compared with Aplysia, is found in the condition of the alimentary canal. The liver is no longer a compact organ opening by a pair of ducts into the median digestive tract, but we find very numerous hepatic diverticula on a shortened axial tract (fig. 66). These diverticula extend usually one into each of the dorsal papillæ or "cerata" when these are present. They are not merely digestive glands, but are sufficiently wide to act as receptacles of food, and in them the digestion of food proceeds just as in the axial portion of the canal. A precisely similar modification of the liver or great digestive gland is found in the Scorpions, where the axial portion of the digestive canal is short and straight, and the lateral ducts sufficiently wide to admit food into the ramifications of the gland there to be digested; whilst in the Spiders the gland is reduced to a series of simple cæca.

The typical character is retained by the heart, pericardium, and the communicating nephridium or renal organ in all Opisthobranchs. An interesting example of this is furnished by the fish-like transparent Phyllirhoë (fig. 58), in which it is possible most satisfactorily to study in the living animal, by means of the microscope, the course of the blood-stream, and also the reno-pericardial communication. With reference to the existence of pores placing the vascular system in open communication with the surrounding water, see the paragraph as to Mollusca generally. In a form closely allied to Aplysia (Pleurobranchus) such a pore leading outwards from the branchial vein has been precisely described by Lacaze Duthiers. No such pore has been detected in Aplysia. In many of the Non-Palliate Opisthobranchs the nervous system presents a concentration of the ganglia (fig. 67), contrasting greatly with what we have seen in Aplysia. Not only are the pleural ganglia fused to the cerebral, but also the visceral to these (see in further illustration the condition attained by the Pulmonate Limnæus, fig. 22), and the visceral loop is astonishingly short and insignificant (fig. 67, *e'*). That the parts are rightly thus identified is probable from Spengel's observation of the osphradium and its nerve-supply in these forms; the nerve to that organ, which is placed somewhat anteriorly—on the dorsal surface—being given off from the hinder part (visceral) of the right compound ganglion—the fellow to that marked A in fig. 67. The Ceratonotous Opisthobranchs, amongst other specialities of structure, are stated to possess (in some cases at any rate) apertures at the apices of the "cerata" or dorsal papillæ, which lead from the exterior into the hepatic cæca. This requires confirmation. Some amongst them (Tergipes, Eolis) are also remarkable for possessing peculiarly modified epidermic cells placed in sacs at the apices of these same papillæ, which resemble the "thread-cells" of the Planarian Flatworms and of the Cœlentera. The existence of these thread-cells is sufficiently remarkable, seeing that the Non-Palliate Opisthobranchs resemble in general form and habit the Planarian worms, many of which also possess thread-cells. But it is not conceivable that their presence is an indication of genetic affinity between the two groups, rather they are instances of homoplasy. The development of many Opisthobranchia has been examined—*e.g.*, Aplysia, Pleurobranchidium, Elysia, Polycera, Doris, Tergipes. All pass through trochosphere and veliger stages, and in all a nautiloid or boat-like shell is developed, preceded by a well-marked "shell-gland" (see figs. 60 and 68). The transition from the free-swimming veliger larva with its nautiloid shell (fig. 60) to the adult form has not been properly observed, and many interesting points as to the true nature of folds (whether epipodia or mantle or velum) have yet to be cleared up by a knowledge of such development in forms like Tethys, Doris, Phyllidia, &c.

As in other Molluscan groups, we find even in closely-allied genera (for instance, in Aplysia and Pleurobranchidium, and other genera observed by Lankester) the greatest differences as to the *amount* of food-material by which the egg-shell is encumbered. Some form their Diblastula by emboly (fig. 7), others by epiboly (fig. 5); and in the later history of the further development of the enclosed cells (arch-enteron) very marked variations occur in closely-allied forms, due to the influence of a greater or less abundance of food-material mixed with the protoplasm of the egg.

Order 2 (of the Euthyneura).—**Pulmonata.**

Characters.—Euthyneurous Anisopleurous Gastropoda, probably derived from ancestral forms similar to the Palliate Opisthobranchia by adaptation to a terrestrial life. The ctenidium is atrophied, and the edge of the mantle-skirt is fused to the dorsal integument by concrescence, except at one point which forms the aperture of the mantle-chamber, thus converted into a nearly closed sac. Air is admitted to this sac for respiratory and hydrostatic purposes, and it thus becomes a lung. An operculum is never present; a contrast being thus afforded with the operculate Pulmonate Streptoneura (Cyclostoma, &c.), which differ in other essential features of structure from the Pulmonata. The Pulmonata are, like the other Euthyneura, hermaphrodite, with elaborately-developed copulatory organs and accessory glands. Like other Euthyneura, they have very numerous small denticles on the lingual ribbon. The ancestral Pulmonata appear to have retained both the right and the left osphradia (Spengel's olfactory organs), since in some (Planorbis, Auricularia) we find the single osphradium to be that of the original left side, whilst in others (Limnæus) it is that of the original right side.

In some Pulmonata (Snails) the foot is extended at right angles to the visceral hump, which rises from it in the form of a coil as in Streptoneura; in others the visceral hump is not elevated, but is extended with the foot, and the shell is small or absent (Slugs).

The Pulmonata are divided into two sub-orders according to the position of the cephalic eyes.

Sub-order 1.—*Basommatophora.*

Characters.—Eyes placed mediad of the cephalic tentacles at their base; the embryonic velar area retained in adult life as a pair of cephalic lobes (fig. 70, *v*); male and female generative apertures separate, placed (as is typical in Anisopleura) on the right side of the neck; visceral hump well developed, with a well-developed shell; aquatic in habit.

Family 1.—*Limnæidæ.*
  Genera: *Limnæus*, Lam. (figs. 3, 4, &c.); *Chilinia*, Gray; *Physa*, Draparn.; *Ancylus*, Geoff.; *Planorbis*, Müll., &c.
Family 2.—*Auriculidæ.*
  Genera: *Auricula*, Lam.; *Conovulus*, Lam.; *Pitharella*, Wood. &c.

Sub-order 2.—*Stylommatophora.*

Characters.—Eyes placed on the summit of two hollow tentacles; visceral hump well or not at all developed; shell large and coiled, or minute or absent; almost exclusively terrestrial.

Family 1.—*Helicidæ.*
  Genera: *Helix*, L. (figs. 69, A; 72*); *Vitrina*, Draparn.; *Succinea*, Draparn.; *Bulimus*, Scopoli; *Achatina*, Lam.; *Pupa*, Lam.; *Clausilia*, Draparn., &c.
Family 2.—*Limacidæ* (Slugs).
  Genera: *Limax*, L.; *Incilaria*, Benson; *Arion*, Ferussac (fig. 69, D); *Parmacella*, Cuvier; *Testacella*, Cuvier (fig. 69, C), &c.
Family 3.—*Oncidiadæ.*
  Genera: *Oncidium*, Buchanan; *Peronia*, Blainv. (fig. 72); *Vaginulus*, Ferussac, &c.

Further Remarks on Pulmonata.—The land-snails and slugs forming the group Pulmonata are widely distinguished from a small set of terrestrial Azygobranchia, the Pneumonochlamyda (see above), at one time associated with them on account of their mantle-chamber being converted, as in Pulmonata, into a lung, and the ctenidium or branchial plume aborted. The Pneumonochlamyda (represented in England by the common genus Cyclostoma) have a twisted visceral nerve-loop, an operculum on the foot, a complex rhipidoglossate or tænioglossate radula, and are of distinct sexes; they are, in fact, Azygobranchiate Streptoneura. The Pulmonata have a straight visceral nerve-loop, never an operculum (even in the embryo), and a multidenticulate radula, the teeth being equi-formal; and they are hermaphrodite. Some Pulmonata (Limnæus, &c.) live in fresh-waters although breathing air. The remarkable discovery has been made that in deep lakes such Limnæi do not breathe air, but admit water to the lung-sac and live at the bottom. The lung-sac serves undoubtedly as a hydrostatic apparatus in the aquatic Pulmonata, as well as assisting respiration. It is not improbable that here, and in other air-breathing animals, the hydrostatic function was the primary one, and the respiratory a later development.

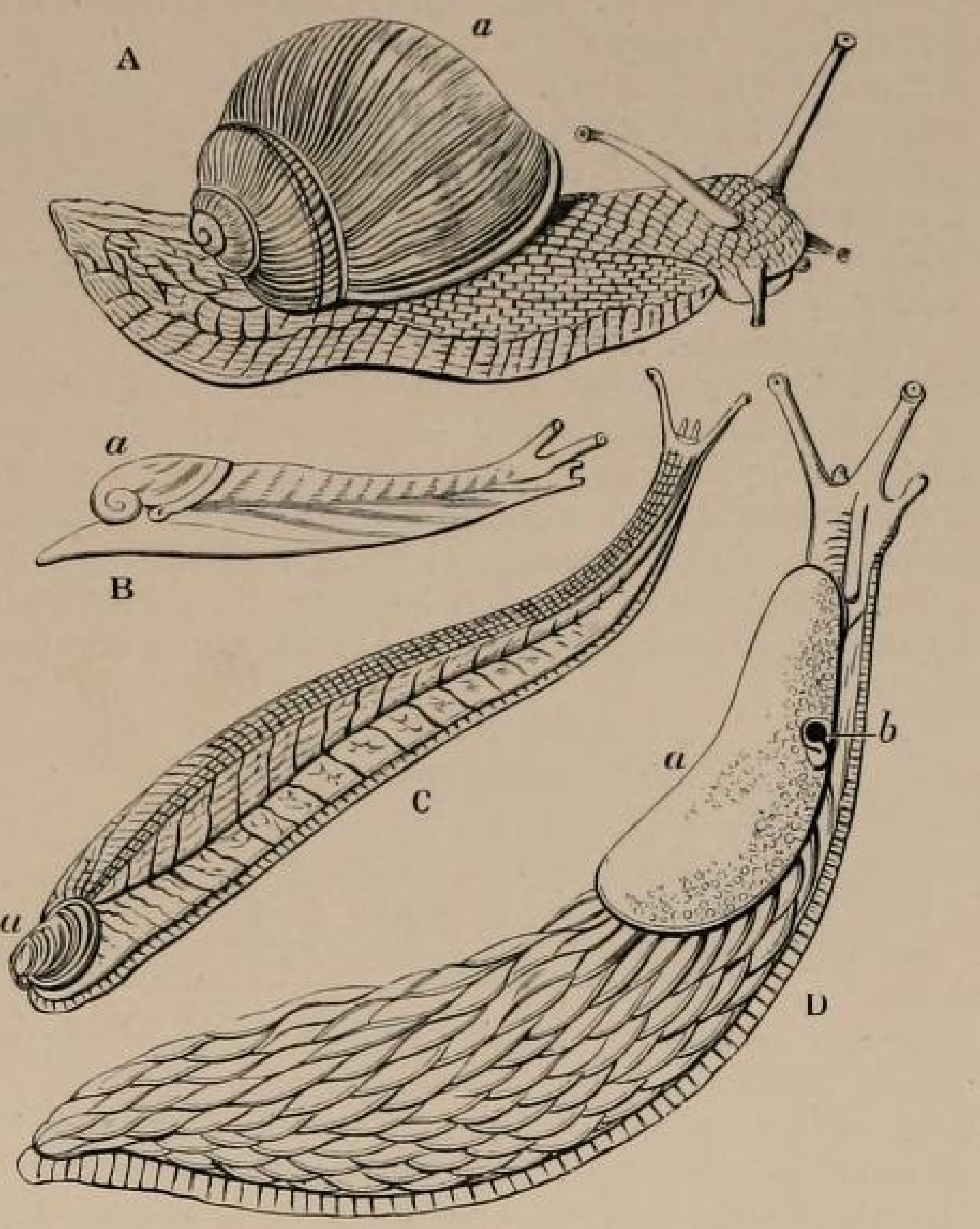


FIG. 69.—A series of Stylommatophorous Pulmonata, showing transitional forms between snail and slug.
A. *Helix pomatia* (from Keferstein).
B. *Helicophanta brevipes* (from Keferstein, after Pfeiffer).
C. *Testacella haliotidea* (from Keferstein).
D. *Arion ater*, the great Black Slug (from Keferstein).
a, Shell in A, B, C, shell-sac (closed) in D; *b*, orifice leading into the subpallial chamber (lung).

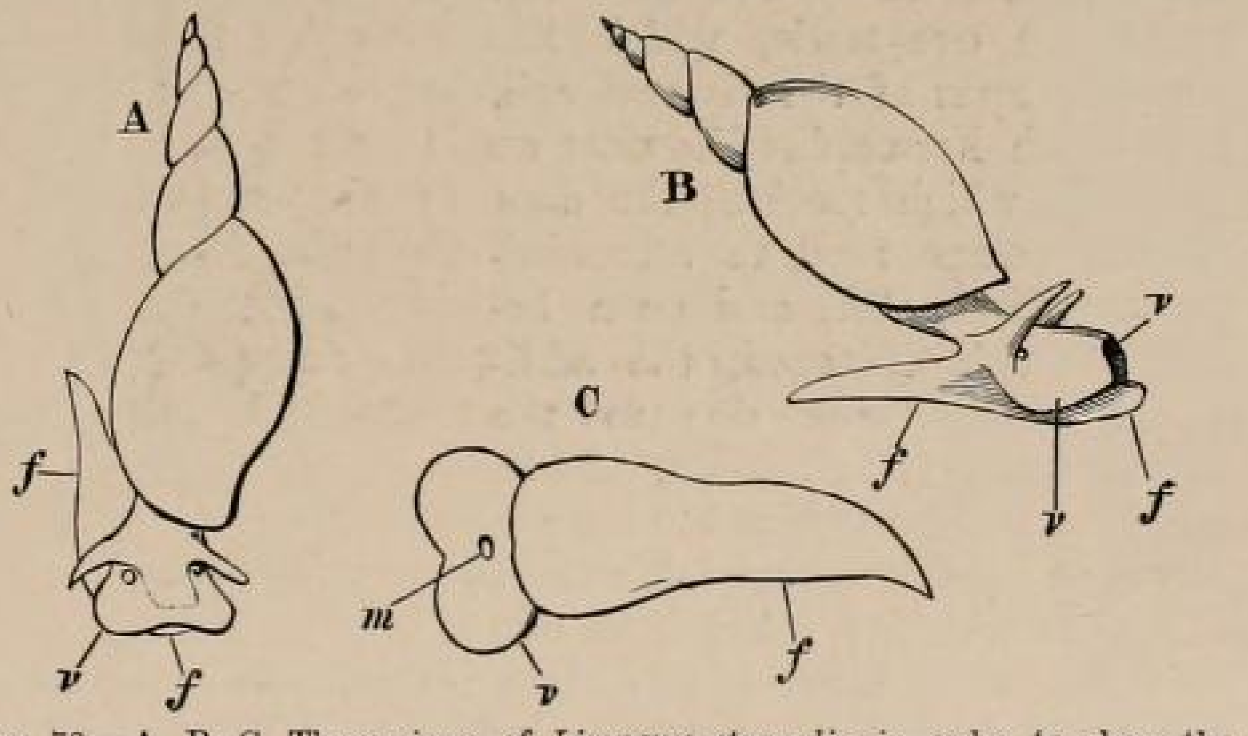


FIG. 70.—A, B, C. Three views of *Limnæus stagnalis*, in order to show the persistence of the larval velar area *v*, as the circum-oral lobes of the adult. *m*, mouth; *f*, foot; *v*, velar area, the margin *v* corresponding with the ciliated band which demarcates the velar area or velum of the embryo Gastropod (see fig. 4, D, E, F, H, I, *v*). (Original.)

The same general range of body-form is shown in Pulmonata as in the Natant Azygobranchia and in the Opisthobranchia; at one extreme we have Snails with coiled visceral hump, at the other cylindrical or flattened Slugs (see fig. 69). Limpet-like forms are also found (fig. 71, Ancylus). The foot is always simple, with its flat crawling surface extending from end to end, but in the embryo Limnæus (fig. 4, H) it shows a bilobed character, which leads on to the condition characteristic of Pteropoda.

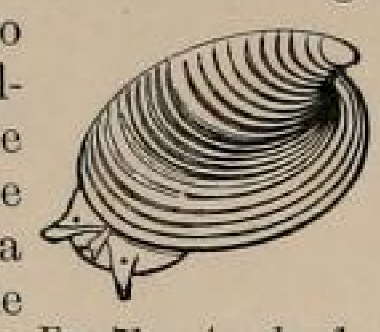


Fig. 71.—*Ancylus fluviatilis*, a patelliform aquatic Pulmonate.

The adaptation of the Pulmonata to terrestrial life has entailed little modification of the internal organization. The vascular system appears to be more complete in them than in other Gastropoda, fine vessels and even capillaries being present in place of lacunæ, in which arteries and veins find their meeting-point. The subject has not, however, been investigated by the proper methods of recent histology, and our knowledge of it, as of the vascular system of Molluscs generally, is most unsatisfactory. In one genus (Planorbis) the plasma of the blood is coloured red by hæmoglobin, this being the only instance of the presence of this body in the blood of Glossophorous Mollusca, though it occurs in corpuscles in the blood of the bivalves Arca and Solen (Lankester, **31**).

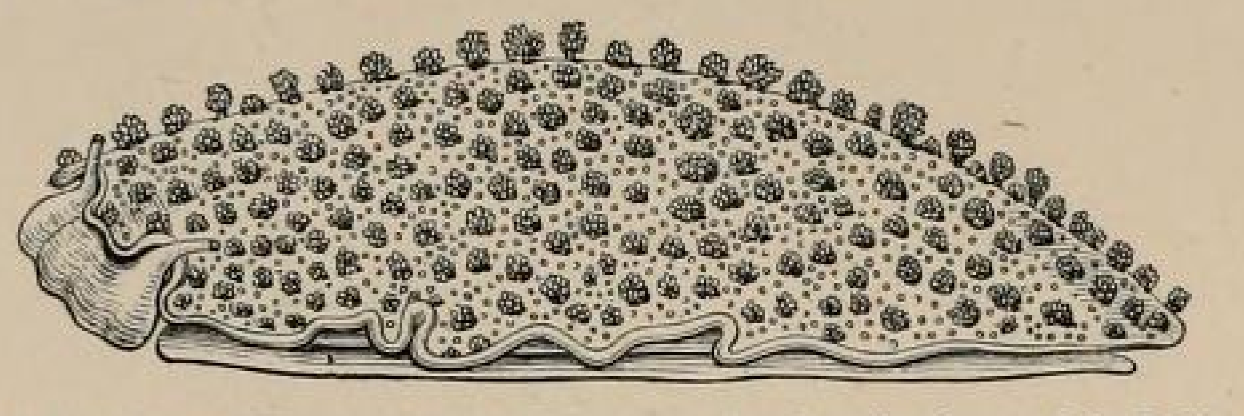


Fig. 72.—*Peronia Tongæ*, a littoral Pulmonate, found on the shores of the Indian and Pacific Oceans (Mauritius, Japan).

The generative apparatus of the Snail (Helix) may serve as an example of the hermaphrodite apparatus common to the Pulmonata and Opisthobranchia (fig. 72*). From the ovo-testis, which lies near the apex of the visceral coil, a common hermaphrodite duct *v.e* proceeds, which receives the duct of the compact white albuminiparous gland *E.d.*, and then becomes much enlarged, the additional width being due to the development of glandular folds, which are regarded as forming a uterus *u*. Where these folds cease the common duct splits into two portions, a male and a female. The male duct *v.d* becomes fleshy and muscular near its termination at the genital pore, forming the penis *p*. Attached to it is a diverticulum *fl.*, in which the spermatozoa which have descended from the ovo-testis are stored and modelled into sperm ropes or spermatophores. The female portion of the duct is more complex. Soon after quitting the uterus it is joined by a long duct leading from a glandular sac, the spermatheca (*R.f*). In this duct and sac the spermatophores received in copulation from another snail are lodged. In *Helix hortensis* the spermatheca is simple. In other species of Helix a second duct (as large in *Helix aspersa* as the chief one) is given off from the spermathecal duct, and in the natural state is closely adherent to the wall of the uterus. This second duct has normally no spermathecal gland at its termination, which is simple and blunt. But in rare cases in *Helix aspersa* a second spermatheca is found at the end of this second duct. Tracing the widening female duct onwards we now come to the openings of the digitate accessory glands *d*, *d*, which probably assist in the formation of the egg-capsule. Close to them is the remarkable dart-sac *ps*, a thick-walled sac, in the lumen of which a crystalline four-fluted rod or dart consisting of carbonate of lime is found. It is supposed to act in some way as a stimulant in copulation, but possibly has to do with the calcareous covering of the egg-capsule. Other Pulmonata exhibit variations of secondary importance in the details of this hermaphrodite apparatus.

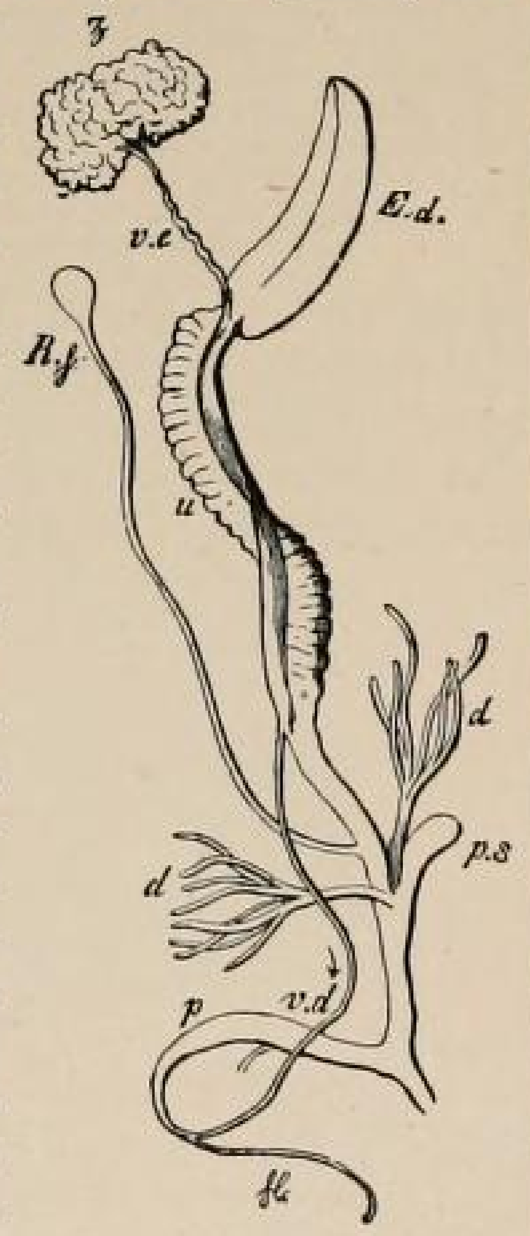


Fig. 72*.—Hermaphrodite reproductive apparatus of the Garden Snail (*Helix hortensis*). *z*, ovo-testis; *v.e*, hermaphrodite duct; *E.d.*, albuminiparous gland; *u*, uterine dilatation of the hermaphrodite duct; *d*, digitate accessory glands on the female duct; *p.s*, calciferous gland or dart-sac on the female duct; *R.f*, spermatheca or receptacle of the sperm in copulation, opening into the female duct; *v.d*, male duct (vas deferens); *p*, penis; *fl.*, flagellum.

The nervous system of Helix is not favourable as an example on account of the fusion of the ganglia to form an almost uniform ring of nervous matter around the œsophagus. The Pond-Snail (Limnæus) furnishes, on the other hand, a very beautiful case of distinct ganglia and connecting cords (fig. 22). The demonstration which it affords of the extreme shortening of the Euthyneurous visceral nerve-loop is most instructive and valuable for comparison with and explanation of the condition of the nervous centres in Cephalopoda, as also of some Opisthobranchia. The figure (fig. 22) is sufficiently described in the letterpress attached to it; the pair of buccal ganglia joined by the connectives to the cerebrals are, as in most of our figures, omitted. Here we need only further draw attention to the osphradium, discovered by Lacaze Duthiers (**32**), and shown by Spengel to agree in its innervation with that organ in all other Gastropoda. On account of the shortness of the visceral loop and the proximity of the right visceral ganglion to the œsophageal nerve-ring, the nerve to the osphradium and olfactory ganglion is very long. The position of the osphradium corresponds more or less closely with that of the vanished right ctenidium, with which it is normally associated. In Helix and Limax the osphradium has not been described, and possibly its discovery might clear up the doubts which have been raised as to the nature of the mantle-chamber of those genera. In Planorbis, which is dexiotropic (as are a few other genera or exceptional varieties of various Anisopleurous Gastropods) instead of being leiotropic, the osphradium is on the left side, and receives its nerve from the left visceral ganglion, the whole series of unilateral organs being reversed. This is, as might be expected, what is found to be the case in all "reversed" Gastropods. It is also the case in the Pulmonate Auricula, which is leiotropic.

The shell of the Pulmonata, though always light and delicate, is in many cases a well-developed spiral "house," into which the creature can withdraw itself; and, although the foot possesses no operculum, yet in Helix the aperture of the shell is closed in the winter by a complete lid, the "hybernaculum," more or less calcareous in nature, which is secreted by the foot. In Clausilia a peculiar modification of this lid exists permanently in the adult, attached by an elastic stalk to the mouth of the shell, and known as the "clausilium." In Limnæus the permanent shell is preceded in the embryo by a well-marked shell-gland or primitive shell-sac (fig. 72***), at one time supposed to be the developing anus, but shown by Lankester to be identical with the "shell-gland" discovered by him in other Mollusca (Pisidium, Pleurobranchidium, Neritina, &c.). As in other Gastropoda Anisopleura, this shell-sac may abnormally develop a plug of chitonous matter, but normally it flattens out and disappears, whilst the cap-like rudiment of the permanent shell is shed out from the dome-like surface of the visceral hump, in the centre of which the shell-sac existed for a brief period.

In Clausilia, according to the observations of Gegenbaur, the primitive shell-sac does not flatten out and disappear, but takes the form of a flattened closed sac. Within this closed sac a plate of calcareous matter is developed, and after a time the upper wall of the sac disappears, and the calcareous plate continues to grow as the nucleus of the permanent shell. In the slug Testacella (fig. 69, C) the shell-plate never attains a large size, though naked. In other slugs, namely, Limax and Arion, the shell-sac remains permanently closed over the shell-plate, which in the latter genus consists of a granular mass of carbonate of lime. The permanence of the primitive shell-sac in these slugs is a point of considerable interest. It is clear enough that the sac is of a different origin from that of Aplysia (described in the section treating of Opisthobranchia), being primitive instead of secondary. It seems probable that it is identical with one of the open sacs in which each shell-plate of a Chiton is formed, and the series of plate-like imbrications which are placed behind the single shell-sac on the dorsum of the curious slug, Plectrophorus, suggest the possibility of the formation of a series of shell-sacs on the back of that animal similar to those which we find in Chiton. Whether the closed primitive shell-sac of the slugs (and with it the transient embryonic shell-gland of all other Mollusca) is precisely the same thing as the closed sac in which the calcareous pen or shell of the Cephalopod Sepia and its allies is formed, is a further question, which we shall consider when dealing with the Cephalopoda. It is important here to note that Clausilia furnishes us with an exceptional instance of the *continuity* of the shell or secreted product of the primitive shell-sac with the adult shell. In most other Mollusca (Anisopleurous Gastropods, Pteropods, and Conchifera) there is a want of such continuity; the primitive shell-sac contributes no factor to the permanent shell, or only a very minute knob-like particle (Neritina and Paludina). It flattens out and disappears before the work of forming the permanent shell commences. And just as there is a break at this stage, so (as observed by Krohn in Marsenia = Echinospira) there *may* be a break at a later stage, the nautiloid shell formed on the larva being cast, and a new shell of a different form being formed afresh on the surface of the visceral hump. It is, then, in this sense that we may speak of primary, secondary, and tertiary shells in Mollusca, recognizing the fact that they *may* be merely phases fused by continuity of growth so as to form but one shell, or that in other cases they *may* be presented to us as separate individual things, in virtue of the non-development of the later phases, or in virtue of sudden changes in the activity of the mantle-surface causing the shedding or disappearance of one phase of shell-formation before a later one is entered upon.

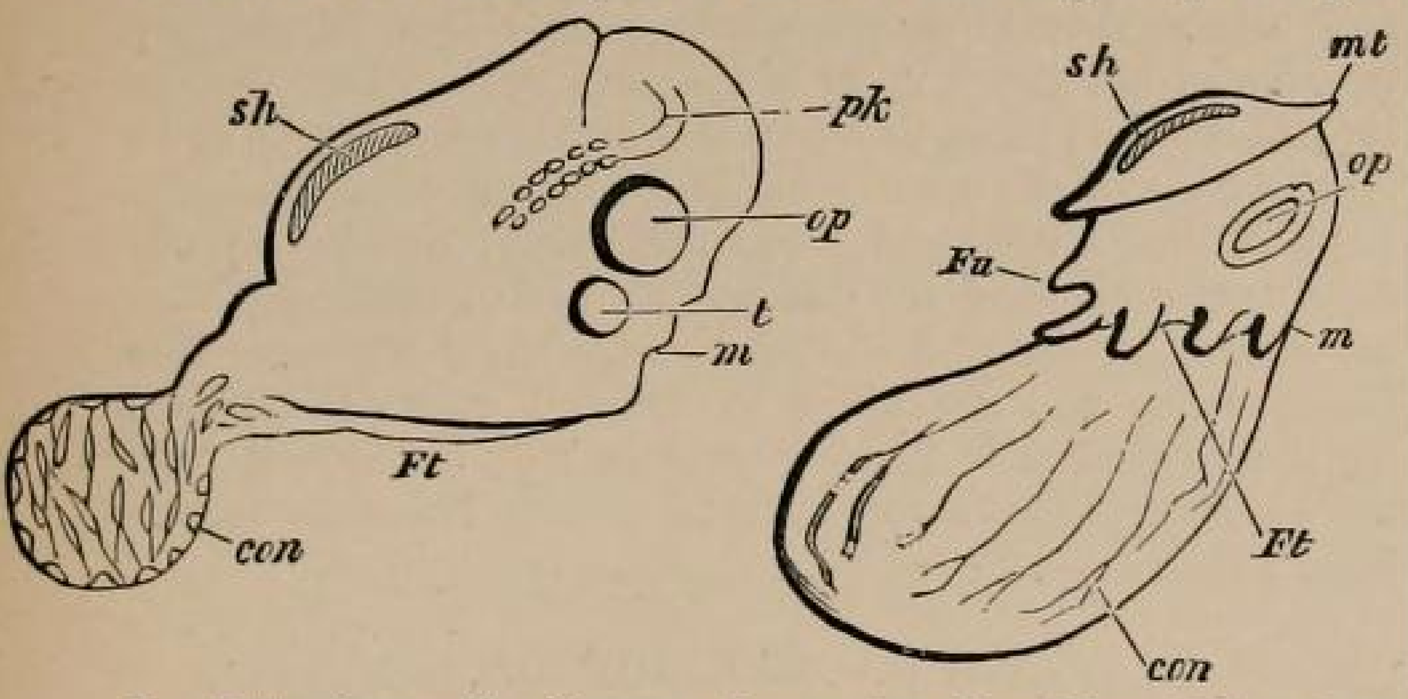


FIG. 72**.—Comparative diagrams of an embryo Slug, Limax (left), and an embryo Cuttle-fish, Loligo (right). *sh*, internal shell; *pk*, embryonic renal organ (Stiebel's canal) in Limax; *mt*, edge of the mantle-flap in Loligo; *op*, cephalic eye; *t*, cephalic tentacle; *m*, position of the mouth; *Ft*, the foot; *Fu*, the hinder part of the foot drawn out to form the funnel of Loligo; *con*, the contractile yelk-sac or hernia-like protrusion of the mid-region of the foot, corresponding to the line of closure of the blastopore in Limnæus. *N.B.*—The blastopore in the embryo of Loligo, which, like that of a bird, is much distorted by excess of food-yelk, *does* close at the extremity of the yelk-sac *con*. (Original.)

The development of the aquatic Pulmonata from the egg offers considerable facilities for study, and that of Limnæus has been elucidated by Lankester, whilst Rabl has with remarkable skill applied the method of sections to the study of the minute embryos of Planorbis. The chief features in the development of Limnæus are exhibited in the woodcuts (figs. 3, 4, and 72***). There is not a very large amount of food-material present in the egg of this snail, and accordingly the cells resulting from division are not so unequal as in many other cases. The four cells first formed are of equal size, and then four smaller cells are formed by division of these four so as to lie at one end of the first four (the pole corresponding to that at which the "directive corpuscles" *dc* are extruded and remain). The smaller cells now divide and spread over the four larger cells (fig. 3); at the same time a space—the cleavage cavity or blastocœl—forms in the centre of the mulberry-like mass. Then the large cells recommence the process of division and sink into the hollow of the sphere, leaving an elongated groove, the blastopore, on the surface (fig. 3, C, and fig, 4, G). The invaginated cells (derived from the division of the four big cells) form the endoderm or arch-enteron; the outer cells are the ectoderm. The blastopore now closes along the middle part of its course, which coincides in position with the future "foot." One end of the blastopore becomes nearly closed, and an ingrowth of ectoderm takes place around it to form the stomodæum or fore-gut and mouth. The other extreme end closes, but the invaginated endoderm cells remain in continuity with this extremity of the blastopore, and form the "rectal peduncle" or "pedicle of invagination" of Lankester (see also the account and figures (fig. 151, A) of the development of the bivalve Pisidium), although the endoderm cells retain no contact with the middle region of the now closed-up blastopore. The anal opening forms at a late period by a very short ingrowth or proctodæum coinciding with the blind termination of the rectal peduncle (fig. 72***, *pi*).

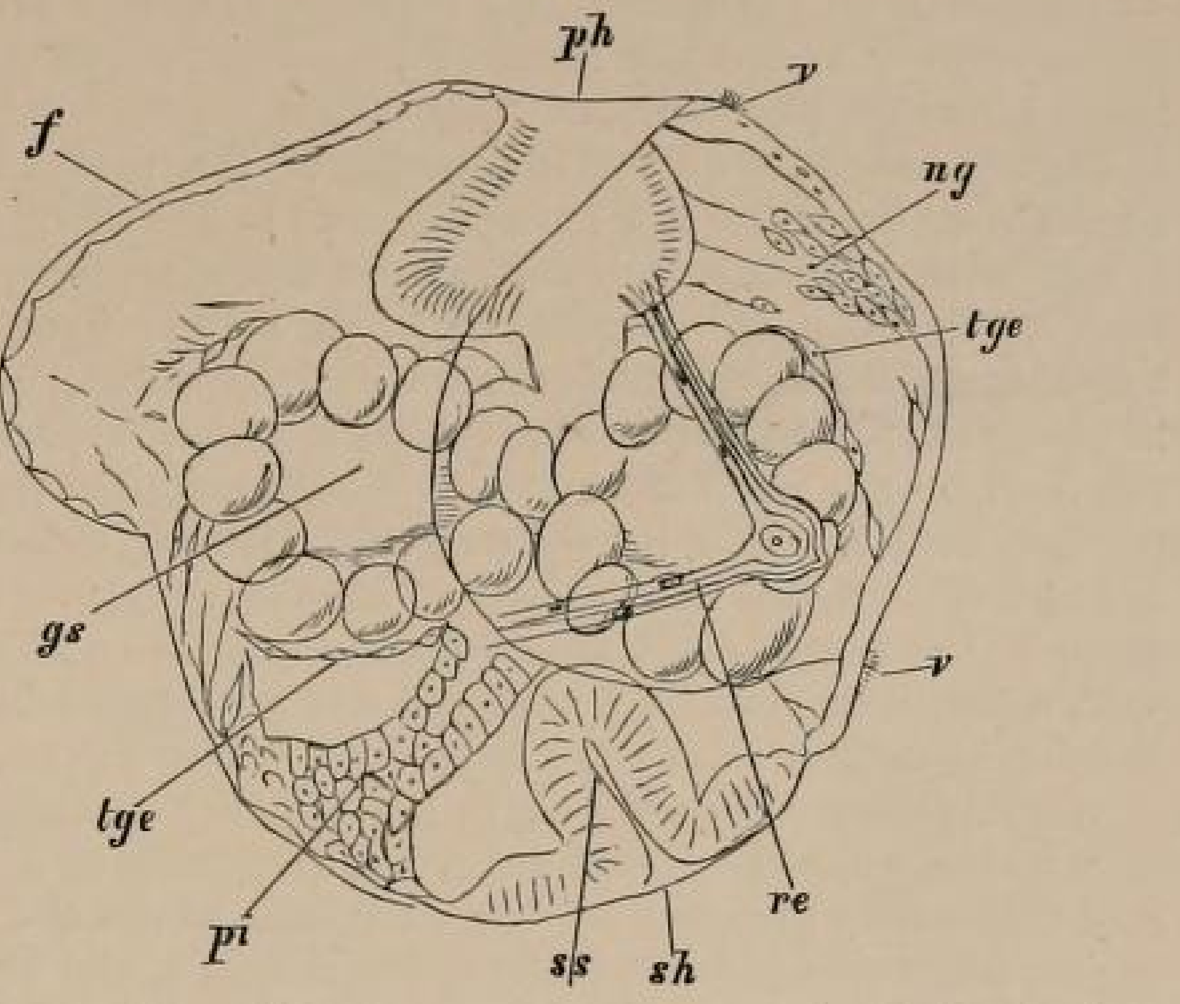


FIG. 72***.—Embryo of *Limnæus stagnalis*, at a stage when the Trochosphere is developing foot and shell-gland and becoming a Veliger, seen as a transparent object under slight pressure. *ph*, pharynx (stomodæal invagination); *v*, *v*, the ciliated band marking out the velum; *ng*, cerebral nerve-ganglion; *re*, Stiebel's canal (left side), probably an evanescent embryonic nephridium; *sh*, the primitive shell-sac or shell-gland; *pi*, the rectal peduncle or pedicle of invagination, its attachment to the ectoderm is coincident with the hindmost extremity of the elongated blastopore of fig. 3, C; *tge*, mesoblastic (skeletotrophic and muscular) cells investing *gs*, the bilobed arch-enteron or lateral vesicles of invaginated endoderm, which will develop into liver; *f*, the foot. (Original.)

The body-cavity and the muscular, fibrous, and vascular tissues are traced partly to two symmetrically-disposed "mesoblasts," which bud off from the invaginated arch-enteron, partly to cells derived from the ectoderm, which at a very early stage is connected by long processes with the invaginated endoderm, as shown in fig. 3, D. The external form of the embryo goes through the same changes as in other Gastropods, and is not, as was held previously to Lankester's observations, exceptional. When the middle and hinder regions of the blastopore are closing in, an equatorial ridge of ciliated cells is formed, converting the embryo into a typical "Trochosphere" (fig. 4, E, F).

The foot now protrudes below the mouth (fig. 4), and the post-oral hemisphere of the Trochosphere grows more rapidly than the anterior or velar area. The young foot shows a bilobed form (fig. 4, D, *f*). Within the velar area the eyes and the cephalic tentacles commence to rise up (fig. 4, D, *t*), and on the surface of the post-oral region is formed a cap-like shell and an encircling ridge, which gradually increases in prominence and becomes the freely depending mantle-skirt. The outline of the velar area becomes strongly emarginated and can be traced through the more mature embryos to the cephalic lobes or labial processes of the adult Limnæus (fig. 70).

This permanence of the distinction of the part known as the velar area through embryonic life to the adult state is exceptional among Mollusca, and is therefore a point of especial interest in Limnæus. None of the figures of adult Limnæus in recent works on Zoology show properly the form of the head and these velar lobes, and accordingly the figures here given have been specially sketched for the present article. The increase of the visceral dome, its spiral twisting, and the gradual closure of the space overhung by the mantle-skirt so as to convert it into a lung-sac with a small contractile aperture, belong to stages in the development later than any represented in our figures.

We may now revert briefly to the internal organization at a period when the Trochosphere is beginning to show a prominent foot growing out from the area where the mid-region of the elongated blastopore was situated, and having therefore at one end of it the mouth and at the other the anus. Fig. 72*** represents such an embryo under slight compression as seen by transmitted light. The ciliated band of the left side of the velar area is indicated by a line extending from *v* to *v*; the foot *f* is seen between the pharynx *ph* and the pedicle of invagination *pi*. The mass of the arch-enteron or invaginated endodermal sac has taken on a bilobed form (compare Pisidium, fig. 151), and its cells are swollen (*gs* and *tge*). This bilobed sac becomes *entirely* the liver in the adult; the intestine and stomach are formed from the pedicle of invagination, whilst the pharynx, œsophagus, and crop form from the stomodæal invagination *ph*. To the right (in the figure) of the rectal peduncle is seen the deeply invaginated shell-gland *ss*, with a secretion *sh* protruding from it. The shell-gland is destined in Limnæus to become very rapidly stretched out, and to disappear. Farther up, within the velar area, the rudiments of the cerebral nerve-ganglion *ng* are seen separating from the ectoderm. A remarkable cord of cells having a position just below the integument occurs on each side of the head. In the figure the cord of the left side is seen, marked *re*. This paired organ consists of a string of cells which are perforated by a duct. The opening of the duct at either end is not known. Such cannulated cells are characteristic of the nephridia of many worms, and it is held that the organs thus formed in the embryo Limnæus are embryonic nephridia. The most important fact about them is that they disappear, and are in no way connected with the typical nephridium of the adult. In reference to their first observer they are conveniently called "Stiebel's canals." Other Pulmonata possess, when embryos, Stiebel's canals in a more fully-developed state, for instance, the common slug Limax (fig. 72**, *pk*). Here too they disappear during embryonic life. Further knowledge concerning them is greatly needed. It is not clear whether there is anything equivalent to them in the embryos of marine Gastropoda or other Mollusca, the ectodermal cells called "embryonic renal organs" in some Gastropod embryos having only a remote resemblance to them. The three pairs of transient embryonic nephridia of the medicinal leech, the ciliated cephalic pits of Nemertines, and the anterior nephridia of Gephyræans, all suggest themselves for comparison with these enigmatical canals.

Marine Pulmonata.—Whilst the Pulmonata are essentially a terrestrial and fresh-water group, there is one genus of slug-like Pulmonates which frequent the sea-coast (Peronia, fig. 72), whilst their immediate congeners (Onchidium) are found in marshes of brackish water. Semper (**33**) has shown that these slugs have, in addition to the usual pair of cephalic eyes, a number of eyes developed upon the dorsal integument. These dorsal eyes are very perfect in elaboration, possessing lens, retinal nerve-end cells, retinal pigment, and optic nerve. Curiously enough, however, they differ from the cephalic Molluscan eye (for an account of which see fig. 118) in the fact that, as in the vertebrate eye, the filaments of the optic nerve penetrate the retina, and are connected with the surfaces of the nerve-end cells nearer the lens instead of with the opposite end. The significance of this arrangement is not known, but it is important to note, as shown by Hensen, Hickson, and others, that in the bivalves Pecten and Spondylus, which also have eyes upon the mantle quite distinct from typical cephalic eyes, there is the same relationship as in Onchidiadæ of the optic nerve to the retinal cells (fig. 145). In both Onchidiadæ and Pecten the pallial eyes have probably been developed by the modification of tentacles, such as coexist in an unmodified form with the eyes. The Onchidiadæ are, according to Semper, pursued as food by the leaping fish Periophthalmus, and the dorsal eyes are of especial value to them in aiding them to escape from this enemy.

Class II.—**SCAPHOPODA.**

Characters.—Mollusca Glossophora with the FOOT adapted to a BURROWING life in sand (figs. 73, 74, *f*). The body, and to a much greater extent the mantle-skirt and the foot, are elongated along the primitive antero-posterior (oro-anal)

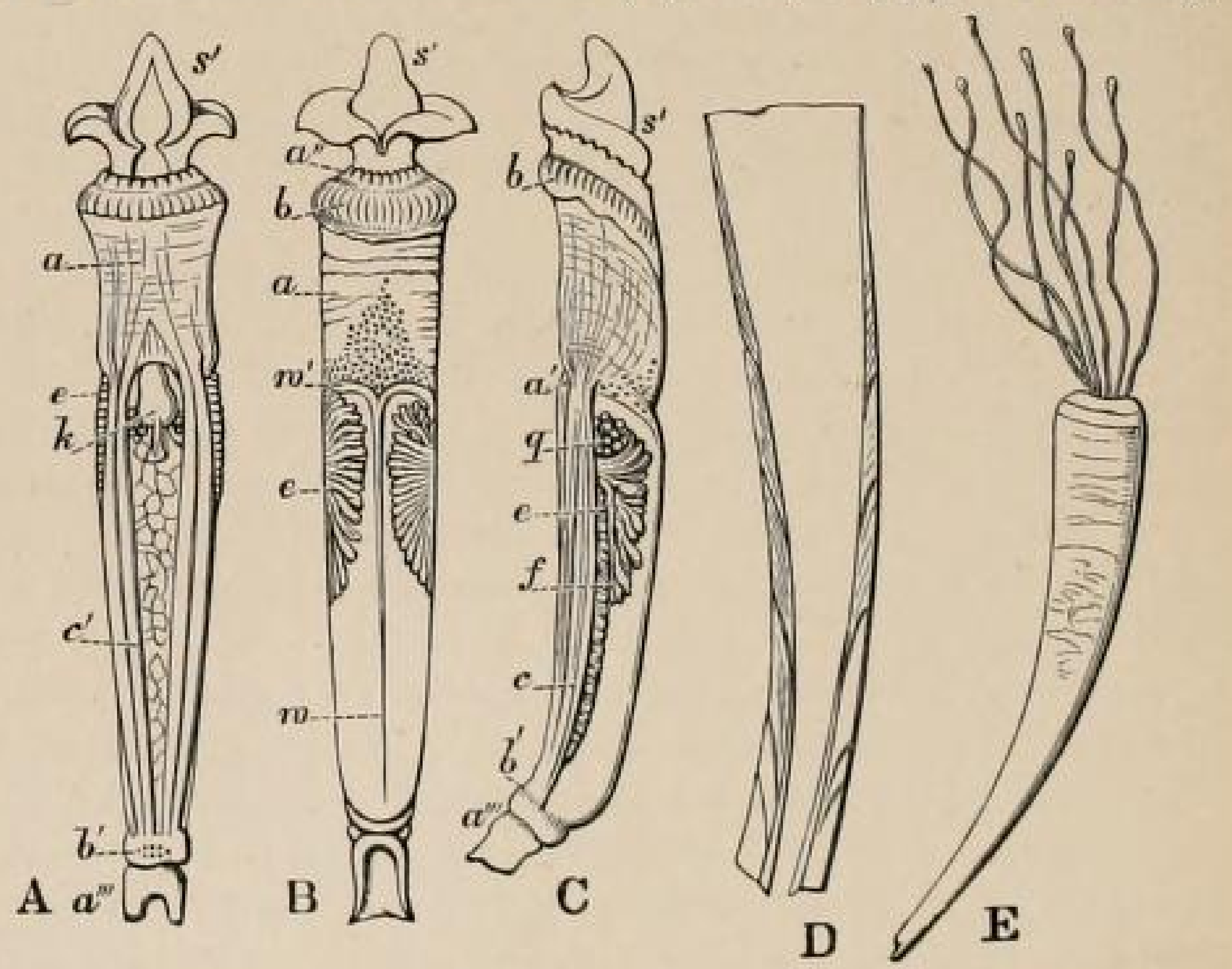


FIG. 73.—*Dentalium vulgare*, Da C. (after Lacaze Duthiers). A. Ventral view of the animal removed from its shell. B. Dorsal view of the same. C. Lateral view of the same. D. The shell in section. E. Surface view of the shell with gill-tentacles exserted as in life. *a*, mantle; *a'*, longitudinal muscle; *a''*, fringe surrounding the anterior opening of the mantle-chamber; *a'''*, the posterior appendix of the mantle; *b*, anterior circular muscle of the mantle; *b'*, posterior do.; *c*, *c'*, longitudinal muscle of mantle; *e*, liver; *f*, gonad; *k*, buccal mass (showing through the mantle); *q*, left nephridium; *s'*, club-shaped extremity of the foot; *w*, *w'*, longitudinal blood-sinus of the mantle.

axis, and retain, both externally and in the disposition of internal organs, the archi-Molluscan BILATERAL SYMMETRY. The margins of the mantle-skirt of opposite sides (right and left) meet below the foot and fuse by concrescence; only a small extent in front and a small extent behind of the mantle-margin is left unfused. Thus a CYLINDRICAL FORM is attained by the mantle, and on its surface a TUBULAR shell (incomplete along the ventral line in the youngest stages) is secreted (fig. 73, D). The FOOT is greatly elongated, and can be protruded from the anterior mantle-aperture. It has a characteristic clavate form (fig. 74, *f*).

The pair of typical CTENIDIA are symmetrically developed in the form of numerous gill-filaments (fig. 74, A, *g*) placed at the base of the cylindrical cephalic prominence or snout (fig. 74, *e*). A pair of NEPHRIDIA (fig. 74, *l*) are present, opening near the anus (fig. 74, *k*). The right serves as a genital duct, the left is apparently renal in function. The LIVER (*p*) is large and bilobed, the lobes divided into parallel lobules. The NERVE-GANGLIA are present (fig. 74, C) as well-marked cerebral, pleural, pedal, and visceral pairs, the typical pleural pair being closely joined to the cerebral. The visceral loop or commissure is untwisted, that is to say, the Scaphopoda are EUTHYNEUROUS. HEART and distinct VESSELS are not developed; a colourless blood is contained in the sinuses and networks formed by the body-cavity. The GONADS are either male or female, the sexes being distinct.

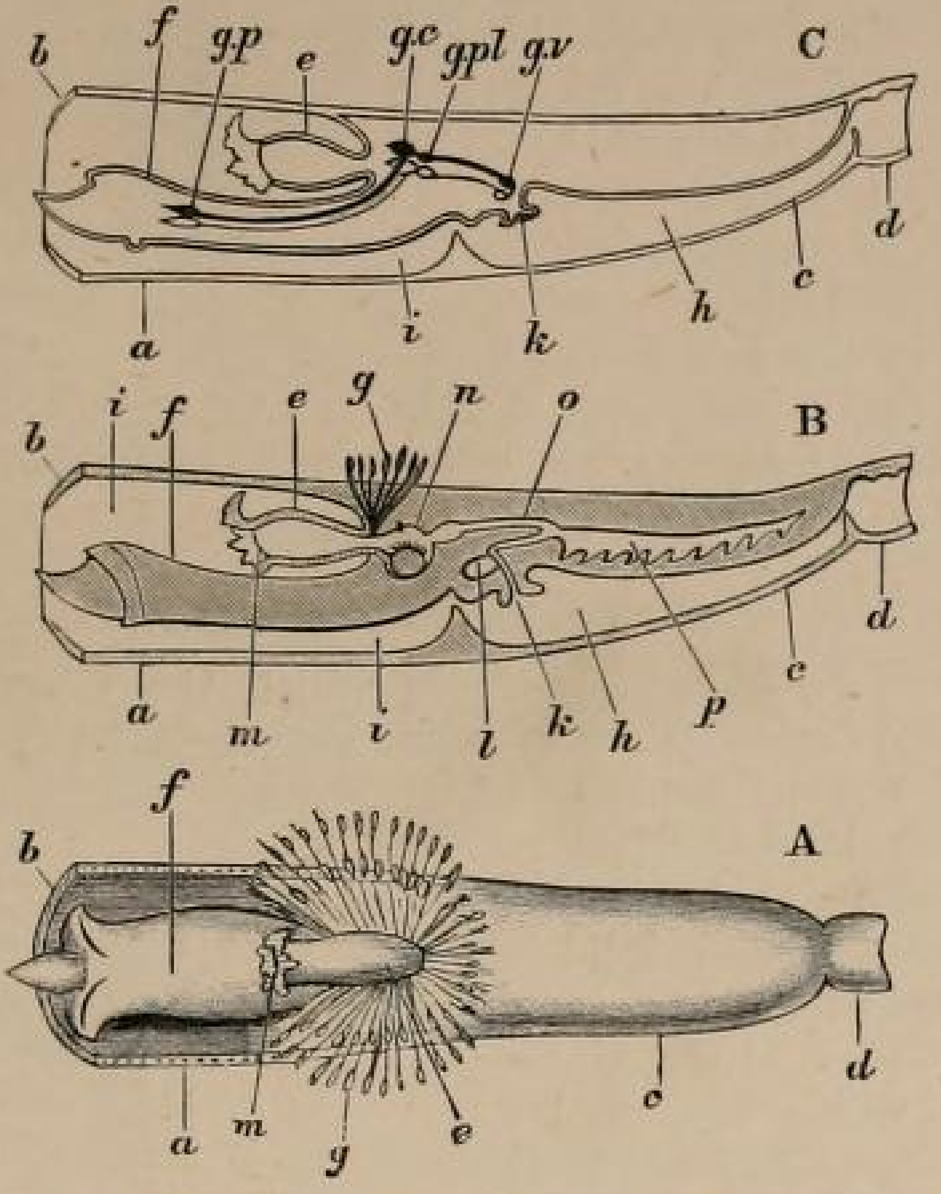


FIG. 74.—Diagrams of the anatomy of Dentalium. A. The anterior portion of the tubular mantle is slit open along the median dorsal line, and its cut margins (*a*) reflected so as to expose the foot, snout, and gills. B. Lateral view with organs showing as though by transparency. C. Similar lateral view to show the number and position of the nerve-ganglia and cords. *a*, the mantle-skirt; *b*, anterior free margin of the same; *c*, hinder extension of the mantle-skirt; *d*, the appendix of the mantle-skirt separated by a valve from the peri-anal portion of the sub-pallial chamber, *h*; *e*, the snout or oral process; *f*, the foot; *g*, the ctenidial filaments; *h*, the peri-anal part of the sub-pallial chamber; *i*, the peri-oral part of the same chamber; *k*, the anus; *l*, the left nephridium; *m*, the mouth surrounded by pinnate tentacles; *n*, the buccal mass and odontophore; *o*, œsophagus; *p*, the left lobe of the liver; *g.p*, pedal ganglion-pair; *g.c*, cerebral ganglion-pair; *g.pl*, pleural ganglion-pair; *g.v*, visceral ganglion-pair. Possibly further research will show that *g.pl* is the typical visceral ganglion-pair, and that *g.v* is a pair of olfactory ganglia placed on the visceral loop as in the Lipocephala according to Spengel.

The embyro is remarkable for developing five ciliated rings posterior to the ciliated ring and tuft characteristic of the trochosphere larval condition of Molluscs generally. These rings are comparable to those of the larva of Pneumodermon (fig. 84), and like them disappear.

The class Scaphopoda is not divisible into orders or families. It contains only three genera: *Dentalium*, L. (figs. 73, 74); *Siphonodentalium*, Sars.; and *Entalium*, Dfr. They inhabit exclusively the sand on the sea-coast in depths of from 10 to 100 fathoms.

It is worthy of remark that the Scaphopoda constitute among the Glossophora a parallel to the sand-boring forms so common among the Lipocephala (such as Solen and Mya). This parallelism is seen in the special mode of elongation of the body, in the form of the foot, and in the tubular form of the mantle brought about by the concrescence of its ventral margins, as in the Lipocephala mentioned. The cylindrical shell of Dentalium is also comparable to the two semi-cylindrical valves of the shell of Solen; or, better, to the tubular shell of Aspergillum and Teredo. Nevertheless, it is necessary to consider the Scaphopoda as standing far apart from the Lipocephala, and as having no special genetic but only a homoplastic relationship to them, in consequence of their possessing a well-developed odontophore, the characteristic organ of the Glossophora never possessed by any Lipocephala.

Class III.—**CEPHALOPODA.**

Characters.—Mollusca Glossophora with the FOOT primarily adapted to a FREE-SWIMMING mode of life. The archi-Molluscan BILATERAL SYMMETRY predominates both in the external and internal organs generally, though in many cases (especially the smaller forms) a one-sided displacement of primitively median organs and a suppression of one of the primitively paired organs is to be noted.

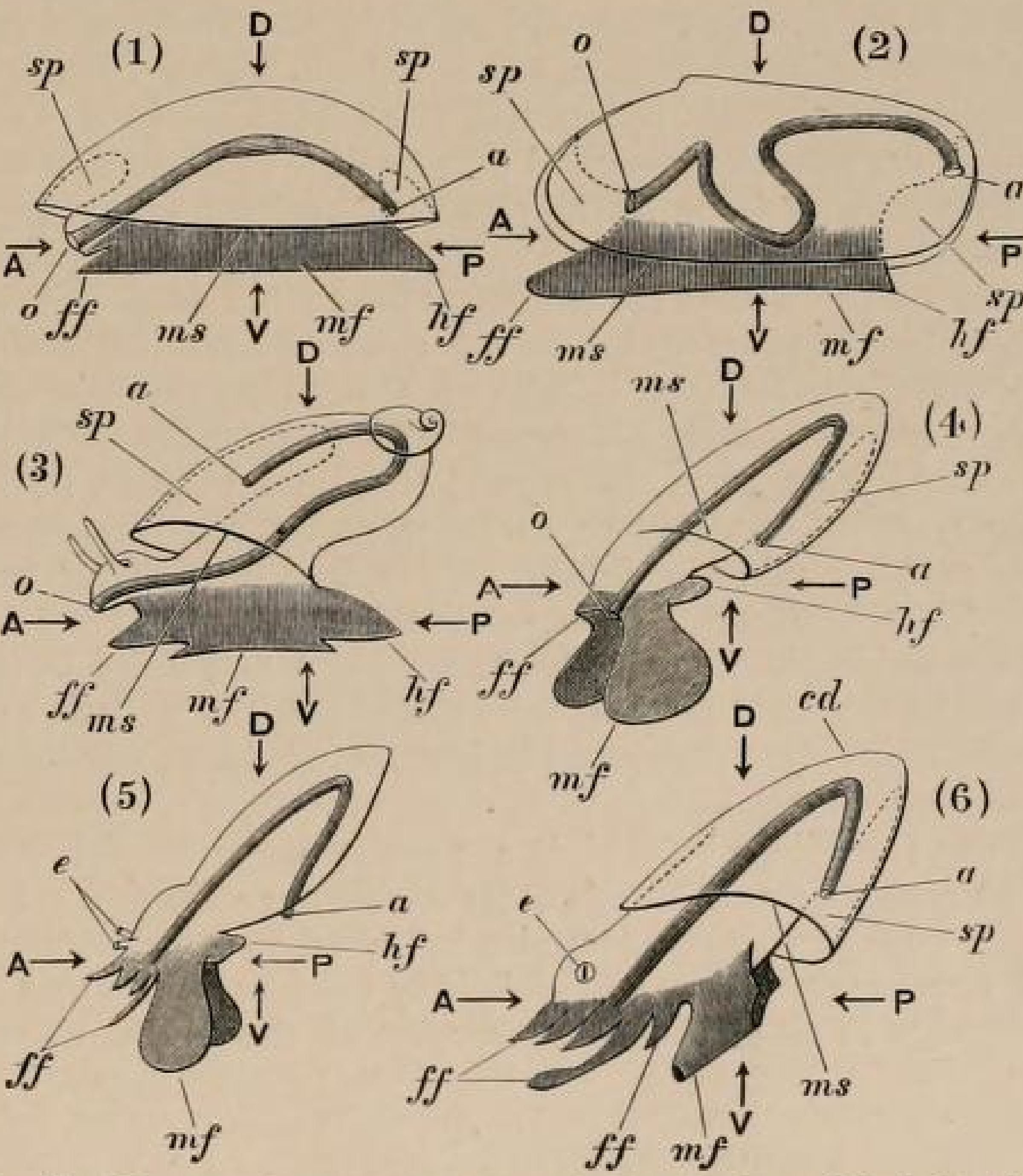


FIG. 75.—Diagrams of a series of Molluscs to show the form of the foot and its regions, and the relation of the visceral hump to the antero-posterior and dorso-ventral axes. (1) A Chiton. (2) A Lamellibranch. (3) An Anisopleurous Gastropod. (4) A Thecosomatous Pteropod. (5) A Gymnosomatous Pteropod. (6) A Siphonopod (Cuttle). A, P, antero-posterior horizontal axis; D, V, dorso-ventral vertical axis at right angles to A, P; *o*, mouth; *a*, anus; *ms*, edge of the mantle-skirt or flap; *sp*, sub-pallial chamber or space; *ff*, fore-foot; *mf*, mid-foot; *hf*, hind-foot; *e*, cephalic eyes; *cd*, centro-dorsal point (in 6 only).

An ANTERIOR, MEDIAN, and POSTERIOR region of the FOOT can be distinguished (fig. 75, (4), (5), (6)), corresponding to but probably not derived from the pro-, meso-, and meta-podium of Gastropoda. The fore-foot invariably has the HEAD MERGED into it, and grows up on each side (right and left) of that part so as to surround the mouth, the two upgrowths of the fore-foot meeting on the dorsal aspect of the snout,—whence the name Cephalopoda. In the more typical forms of both branches of the class, the peri-oral portion of the foot is drawn out into paired arm-like processes, either very short and conical (Clio, Eurybia), or lengthy (Pneumodermon, Octopus); these may be beset with suckers or hooks, or both. The mid-foot (fig. 75, *mf*) is expanded into a pair of muscular lobes right and left, which either are used for striking the water like the wings of a butterfly (Pteropoda), or are bent round towards one another so that their free margins meet and constitute a short tube,—the siphon or funnel (Siphonopoda). The hind foot is either very small or absent.

A distinctive feature of the Cephalopoda is the ABSENCE of anything like the TORSION of the visceral mass seen in the Anisopleurous Gastropoda, although as an exception this torsion occurs in one family (the Limacinidæ).

The ANUS, although it may be a little displaced from the median line, is (except in Limacinidæ) approximately median and posterior. The MANTLE-SKIRT may be aborted (Gymnosomatous Pteropoda); when present it is deeply produced posteriorly, forming a large sub-pallial chamber around the anus. As in our schematic Mollusc, by the side of the anus are placed the single or paired apertures of the NEPHRIDIA, the GENITAL APERTURES (paired only in Nautilus, in female Octopoda, female Ommastrephes, and male Eledone), and the paired CTENIDIA (absent in all Pteropoda). The VISCERAL HUMP or dome is elevated, and may be very much elongated (see fig. 75, (4), (5), (6)) in a direction almost at right angles to the primary horizontal axis (**A**, **P** in fig. 75) of the foot.

A SHELL is frequently, but not invariably, secreted on the visceral hump and mantle-skirt of Cephalopoda; but there are both Pteropoda and Siphonopoda devoid of any shell. The shell is usually light in substance or lightened by air-chambers in correlation with the free-swimming habits of the Cephalopoda. It may be external, when it is box-like or boat-like, or internal, when it is plate-like. Very numerous minute pigmented sacs capable of expansion and contraction, and known as CHROMATOPHORES, are usually present in the integument in both branches of the class. The GONADS of both sexes are developed in one individual in some Cephalopoda (Pteropoda), in others the sexes are separate.

SENSE-ORGANS, especially the cephalic eyes and the otocysts, are very highly developed in the higher Cephalopoda. The osphradia have the typical form and position in the lower forms, but appear to be more or less completely replaced by other olfactory organs in the higher. The normal NERVE-GANGLIA are present, but the connectives are shortened, and the ganglia concentrated and fused in the cephalic region. Large special ganglia (optic, stellate, and supra-buccal) are developed in the higher forms (Siphonopoda).

The Cephalopoda exhibit a greater range from low to high organization than any other Molluscan class, and hence they are difficult to characterize in regard to several groups of organs; but they are definitely held together by the existence in all of the encroachment of the fore-foot so as to surround the head, and by the functionally important BILOBATION OF THE MID-FOOT.

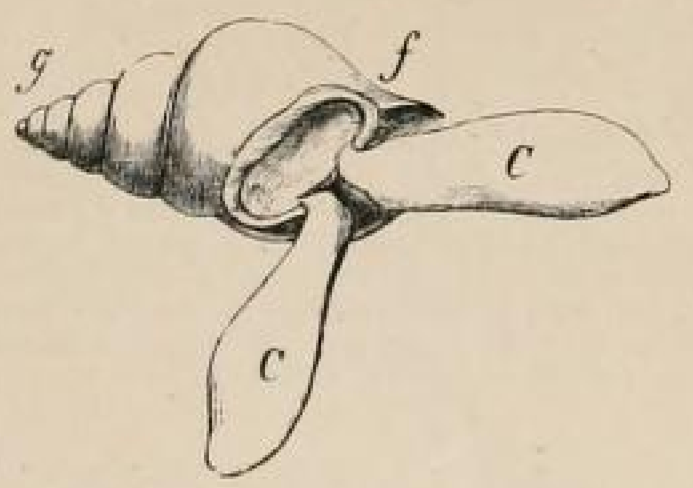


Fig. 76.

Fig. 77.

FIG. 76.—*Spirialis bulimoides*, Soul., one of the Limacinidæ enlarged (from Owen). *C C*, pteropodial lobes of the mid-foot; *f*, operculum carried on the hind-foot; *g*, spiral shell.
FIG. 77.—Operculum of Spirialis enlarged.

Two very distinct branches of the Cephalopoda are to be recognized: the one, the Pteropoda, more archaic in the condition of its bilobed mid-foot, including a number of minute, and in all probability degenerate, oceanic forms of simplified and obscure organization; the other, the Siphonopoda, containing the Pearly Nautilus and the Cuttles, which have for ages (as their fossil remains show) dominated among the inhabitants of the sea, being more highly gifted in special sense, more varied in movement, more powerful in proportion to size, and more heavily equipped with destructive weapons of offence than any other marine organisms.

FIG. 77*a*.—*Cymbulia Peronii*, Cuvier (from Owen). *C*, *C*, the expanded pteropodial lobes or wing-like fins of the mid-foot.

Branch *a*.—*PTEROPODA*.

Characters.—Cephalopoda in which the mid-region of the foot is (as compared with the Siphonopoda) in its more primitive condition, being relatively largely developed and drawn out into a pair of wing-like muscular lobes (identical with the two halves of the siphon of the Siphonopoda) which are used as paddles (see figs. 76-86). The hind-region of the foot is often aborted, but may carry an operculum (figs. 76, 77). The fore-region of the foot (that embracing the head) is also often rudimentary, but may be drawn out into one or more pairs of tentacles, simulating cephalic tentacles, and provided with suckers (figs. 84, 85).

Though the visceral hump is not twisted except in the Limacinidæ (fig. 76), there is a very general tendency to one-sided development of the viscera, and of their external apertures (as contrasted with Siphonopoda). The ctenidia are aborted, with the possible exception of the processes (fig. 85, *c*) at the end of the body of Pneumodermon. The vascular system resembles that of the Gastropoda. The nephridium is a single tubular body corresponding to the right nephridium of the typical pair of the archi-Mollusc. The anal aperture is usually placed a little to the left of the median line, more rarely to the right. In the Limacinidæ it has an exceptional position, owing to the torsion of the visceral mass, as in Anisopleurous Gastropoda.

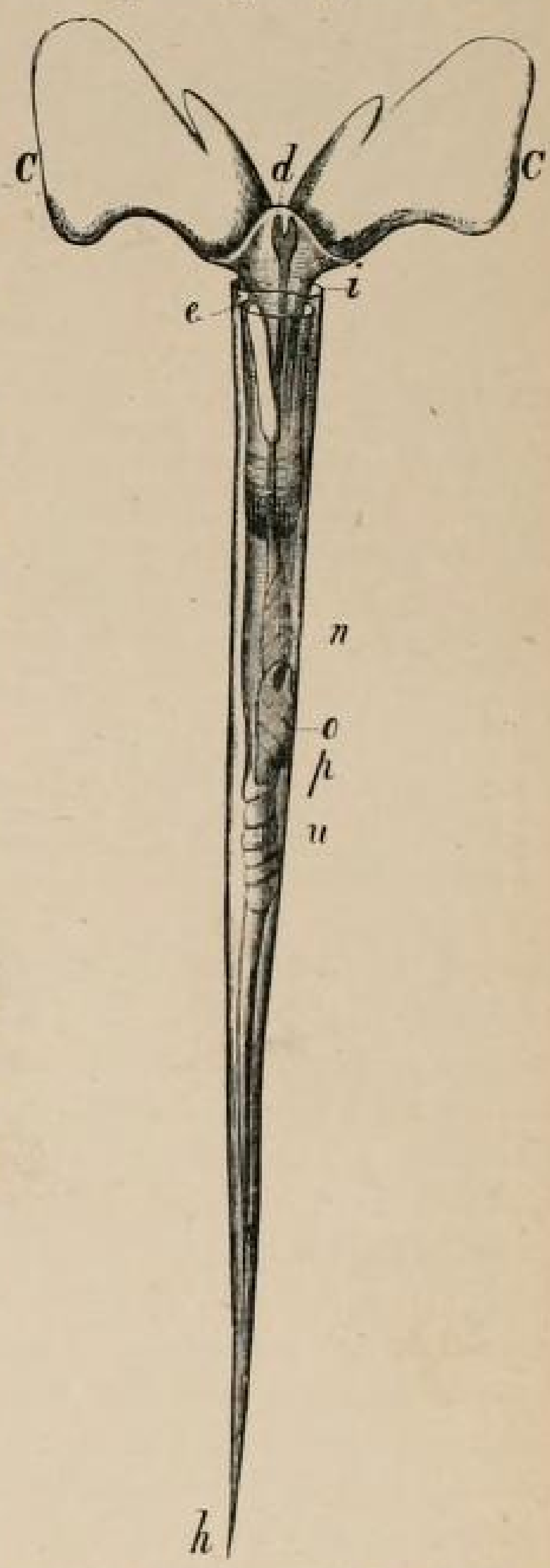


FIG. 78.—*Styliola acicula*, Rang. sp. enlarged (from Owen). *C*, *C*, the wing-like lobes of the mid-foot; *d*, median fold of same; *e*, copulatory organ; *h*, pointed extremity of the shell; *i*, anterior margin of the shell; *n*, stomach: *o*, liver; *u*, hermaphrodite gonad.

Jaws and a lingual ribbon are present as in typical Glossophora, the dentition of the ribbon and the number of jaw-pieces presenting a certain range of variation. Sense-organs are present in the form of cephalic eyes in very few forms (Cavolinia, Clione, and in an undescribed form discovered by Suhm during the "Challenger" Expedition); otocysts are universally present. The osphradia are present in typical form, although the ctenidia are aborted; only one osphradium (the right of the typical pair) is present (fig. 87). The gonads are both male and female in the same individual. The genital aperture is single. Copulatory organs, often of considerable size, are present (fig. 86, *z*).

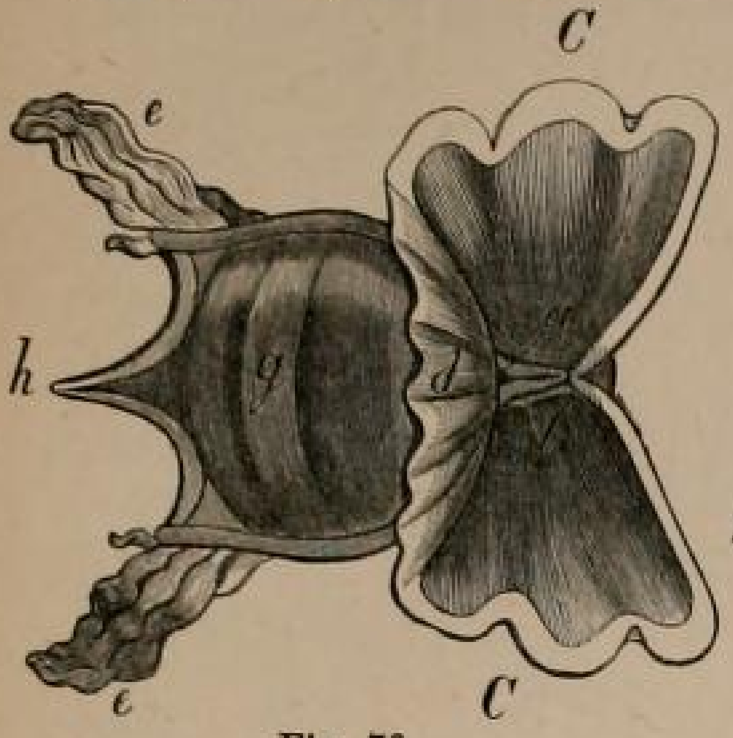


Fig. 79.

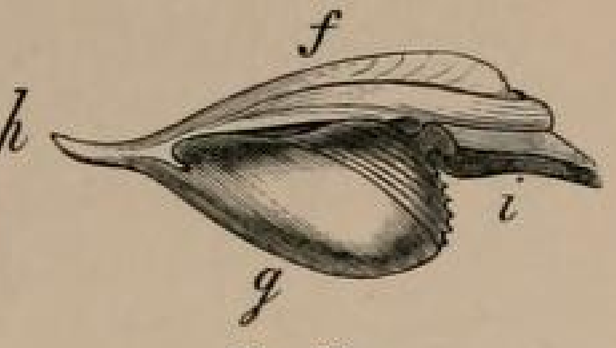


Fig. 80.

FIG. 79.—*Cavolinia tridentata*, Forsk. from the Mediterranean, magnified two diameters (from Owen). *a*, mouth; *b*, pair of cephalic tentacles; *C*, *C*, pteropodial lobes of the mid-foot; *d*, median web connecting these; *e*, *e*, processes of the mantle-skirt reflected over the surface of the shell; *g*, the shell enclosing the visceral hump; *h*, the median spine of the shell.

FIG. 80.—Shell of *Cavolinia tridentata*, seen from the side. *f*, postero-dorsal surface; *g*, antero-ventral surface; *h*, median dorsal spine; *i*, mouth of the shell.

The mantle-skirt is present in one division of the Pteropoda (Thecosomata), and in these an extensive sub-pallial chamber is developed, the walls of which in the absence of ctenidia have a branchial function. In a second division (Gymnosomata), which comprises forms highly developed in regard to the processes of the fore-foot, the mantle-skirt is aborted. A shell is developed on the surface of the visceral hump and mantle-skirt of the Thecosomata, whilst in the Gymnosomata, which have no mantle-skirt, there is in the adult animal no shell. The embryo passes through a trochosphere and a veliger stage (fig. 81), provided with boat-like shell, except in some Gymnosomata in which the Trochosphere with its single velar ciliated band becomes metamorphosed into a larva which has three additional ciliated bands but no velum (resembling the larva of the Scaphopod Dentalium); this banded larva does *not* form a larval shell (fig. 84).

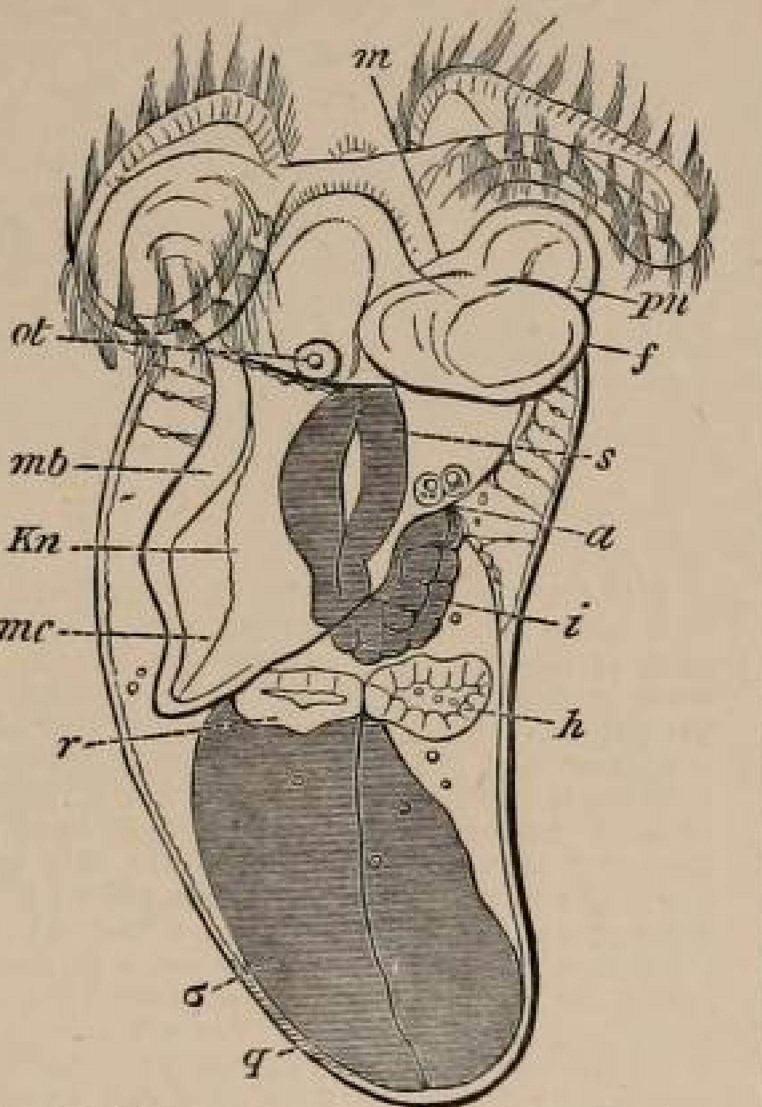


FIG. 81.—Embryo of *Cavolinia tridentata* (from Balfour, after Fol.). *a*, anus; *f*, median portion of the foot; *pn*, pteropodial lobe of the foot; *h*, heart; *i*, intestine; *ot*, otocyst; *q*, shell; *r*, nephridium; *s*, œsophagus; *σ*, sac containing nutritive yelk; *mb*, mantle-skirt; *mc*, sub-pallial chamber; *Kn*, contractile sinus.

The Pteropoda are divided into two orders.

Order 1.—**Thecosomata.**

Characters.—Pteropoda provided with a mantle-skirt, and with a delicate hyaline shell developed on the surface of the visceral hump and mantle-skirt; visceral hump, and consequently the shell, spirally twisted in one family, the Limacinidæ; shell often with contracted mouth and dilated body, its walls sometimes drawn out into spine-like processes, which are covered by reflexions of the free margin of the mantle (Cavolinia, figs. 79, 80).

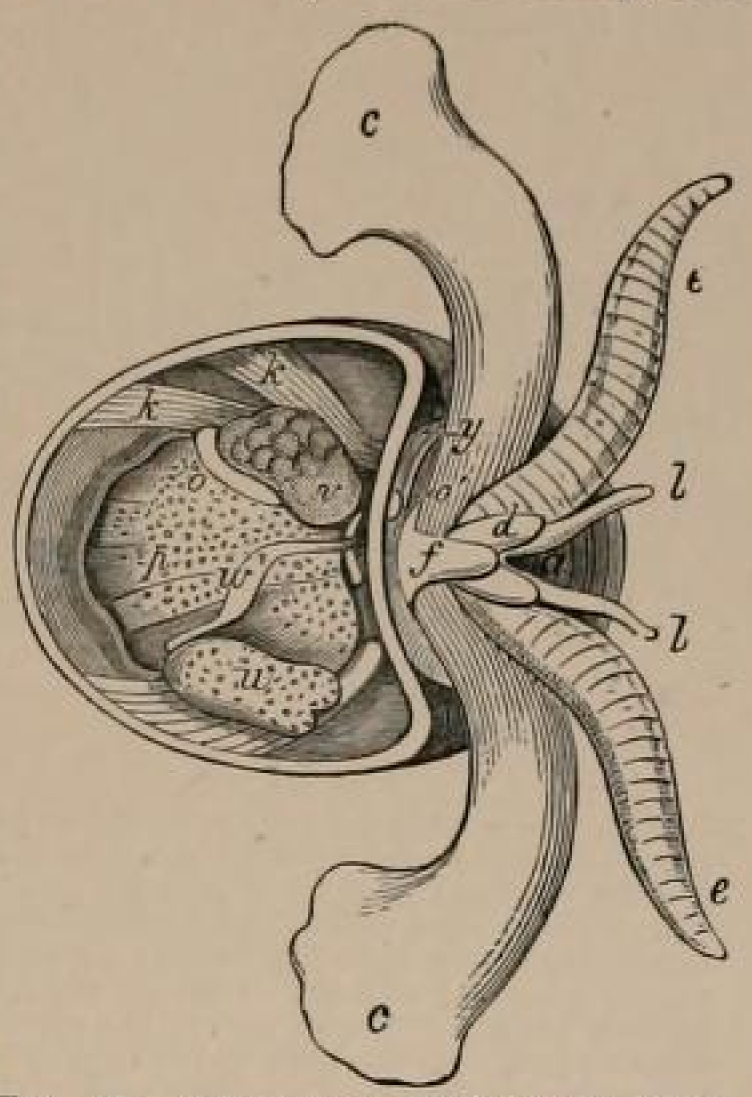


FIG. 82.—*Theceurybia Gaudichaudii*, Soul., (from Owen). Much enlarged; the body-wall removed. *a*, the mouth; *c*, the pteropodial lobes of the foot; *f*, the centrally-placed hind-foot; *d*, *l*, *e*, three pairs of tentacle-like processes placed at the sides of the mouth, and developed (in all probability) from the fore-foot; *o'*, anus; *y*, genital pore; *k*, retractor muscles; *o* and *p*, the liver; *u*, *v*, *w*, genitalia.

Family 1.—*Cymbuliidæ*.
  Genera: *Tiedemannia*, Chj.; *Halopsyche*, *Theceurybia* (figs. 82, 83), *Cymbulia*, P. and L. (fig. 77*a*).
Family 2.—*Conulariidæ* (fossil).
  Genus: *Conularia*, Mill.
Family 3.—*Tentaculitidæ* (fossil).
  Genera: *Tentaculites*, Schlth.; *Cornulites*, Schlth.; *Coleoprion*, Sandb.
Family 4.—*Hyaleidæ*.
  Genera: *Triptera*, Q. and G.; *Styliola*, Les. (fig. 78); *Balantium*, Lch.; *Vaginella*, Dand.; *Cleodora*, P. and L.; *Diacria*, Gr.; *Pleuropus*, Esch.; *Cavolinia*, Gioni. (figs. 79, 80, 81).
Family 5.—*Thecidæ*.
  Genera: *Theca*, Low; *Pterotheca*, Salt.
Family 6.—*Limacinidæ*.
  Genera: *Eccyliomphalus*, Porti.; *Heterofusus*, Flg.; *Spirialis*, E. S. (fig. 76); *Limacina*, Cuv.

Order 2.—**Gymnosomata.**

Characters.—Pteropoda devoid of mantle-skirt and shell; tentacular processes of the fore-foot well developed and provided with suckers.

Family 1.—*Pterocymodoceidæ*.
  Genus: *Pterocymodoce*, Kef.
Family 2.—*Clionidæ*.
  Genera: *Cliodita*, Q. and G.; *Clionopsis*, Trosch.; *Clione*, Pall. (fig. 86).
Family 3.—*Pneumodermidæ*.
  Genera: *Trichocyclus*, Esch.; *Spongobranchia*, d'Orb.; *Pneumodermopsis*, Kef.; *Pneumodermon*, Cuv. (fig. 85).

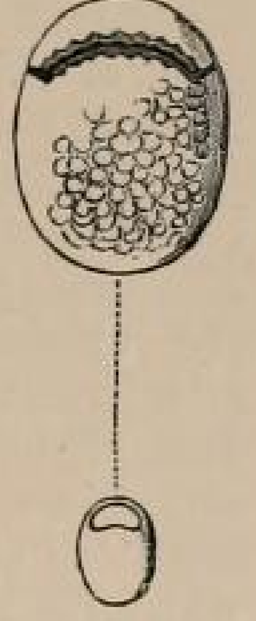


FIG. 83.—Shell of *Theceurybia norfolkensis*; the lower figure shows the natural size.

Branch *b*.—*SIPHONOPODA*.

Cephalopoda in which the two primarily divergent right and left lobes of the mid-region of the foot have their free borders recurved towards the middle line, where they are either held in apposition (Tetrabranchiata), or fused with one another to form a complete cylinder open at each end (Dibranchiata). This fissured or completely closed tube is the siphon (fig. 75, (6), *mf*) characteristic of the Siphonopoda, and is used to guide the stream of water expelled by the contractions of the walls of the branchial chamber. The pallial skirt is accordingly well developed and muscular, subserving by its contractions not only respiration but locomotion. The visceral hump is never twisted, and accordingly the main development of the pallial skirt and chamber is posterior, the excretory apertures, anus, and gills having a posterior position, as in the archi-Mollusc. At the same time the visceral hump is usually much elongated in a direction corresponding to an oblique line between the vertical dorso-ventral and the horizontal antero-posterior axes (see fig. 75, (6)).

The fore-part of the foot which surrounds the mouth, as in all Cephalopoda, is drawn out into four or five pairs of lobes, sometimes short, but usually elongated and even filiform. These lobes either carry peculiar sheathed tentacles (Nautilus), or, on the other hand, acetabuliform suckers, which may be associated with claw-like hooks (Dibranchiata). The hind-foot is probably represented by the valve which depends from the inner wall of the siphon in many cases.

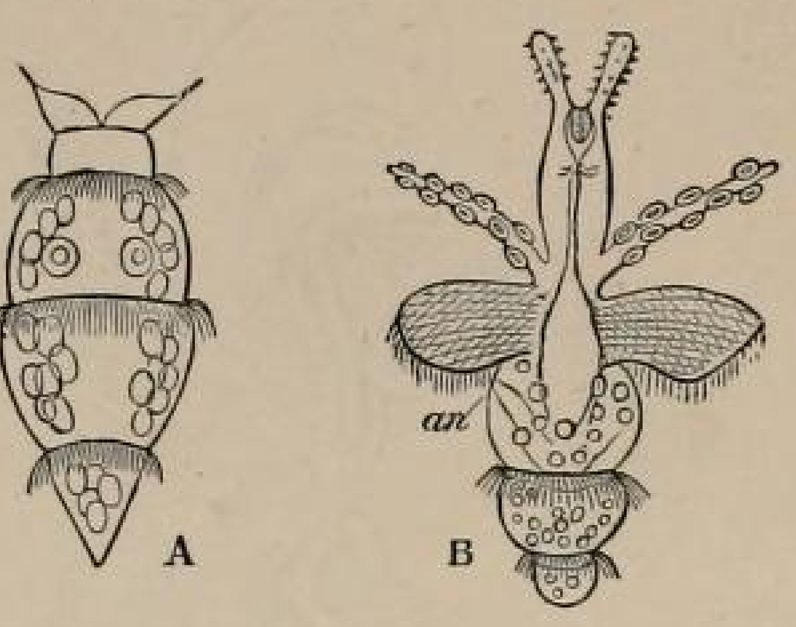


Fig. 84.

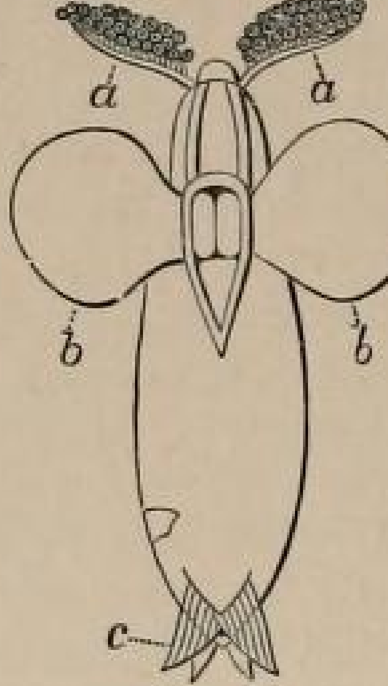


Fig. 85.

Fig. 84.—Larvæ of Pneumodermon (from Balfour, after Gegenbaur). The præ-oral ciliated band of the trochosphere stage (velum) has atrophied. In A three post-oral circlets of cilia are present. The otocysts are seen, and the rudiments of a pair of processes growing from the head. In B the foremost ciliated ring has disappeared; the cephalic region is greatly developed, and, as compared with the adult (fig. 85), is large and free; the pair of hook-bearing processes on each side of the mouth are retractile, probably part of the fore-foot. At the base of the cephalic snout are seen the pair of arm-like processes (fore-foot) provided with suckers, and behind these the broad pteropodial lobes or wing-like fins of the mid-foot.

Fig. 85.—*Pneumodermon violaceum*, d'Orb.; magnified five diameters. *a*, the sucker-bearing arms; *b*, the fins of the mid-foot (in the middle line, between these, is seen the sucker-like median portion of the foot, by means of which the animal can crawl as a Gastropod); *c*, the four branchial processes. (After Keferstein.)

A shell (figs. 89, 100) is very generally present, affording protection to the visceral mass and attachment for muscles. It may be external or enclosed in dorsal upgrowing folds of the mantle, which (except in Spirula) close up at an early period of development, so as to form a shut sac in which the shell is secreted. The ctenidia are well developed as paired gill-plumes, serving as the efficient branchial organs (figs. 101, 103, and fig. 2, B).

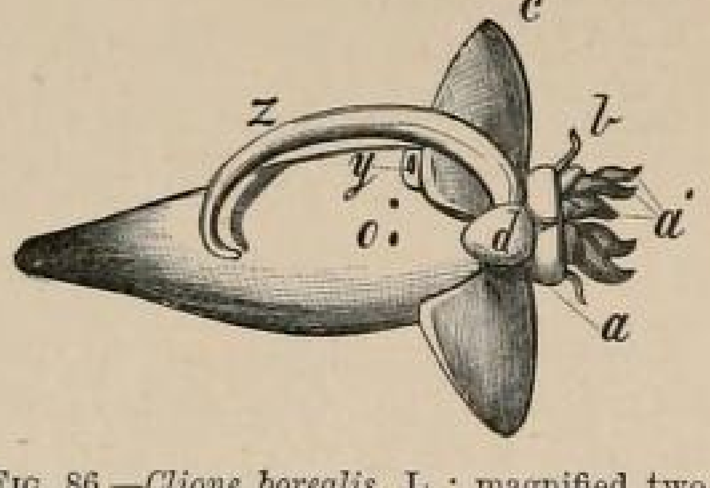


Fig. 86.—*Clione borealis*, L.; magnified two diameters,—postero-ventral aspect. *a*, the cephalic region carrying *a'*—three pairs of cephalic cones provided each with very numerous minute sucker-like processes, and surrounded by a hood-like upgrowth,—and *b*, the more elongated tentacles (the retractile eye-tentacles are not seen, being placed dorsally); *c*, the pteropodial fins; *d*, the median portion of the foot; *o*, the anus; *y*, the vagina; *z*, the penis. (From Owen, after Eschricht.)

The vascular system is very highly developed; the heart consists of a pair of auricles and a ventricle (figs. 104, 105). Branchial hearts are formed on the advehent vessels of the branchiæ. It is not known to what extent the minute subdivision of the arteries extends, or whether there is a true capillary system.

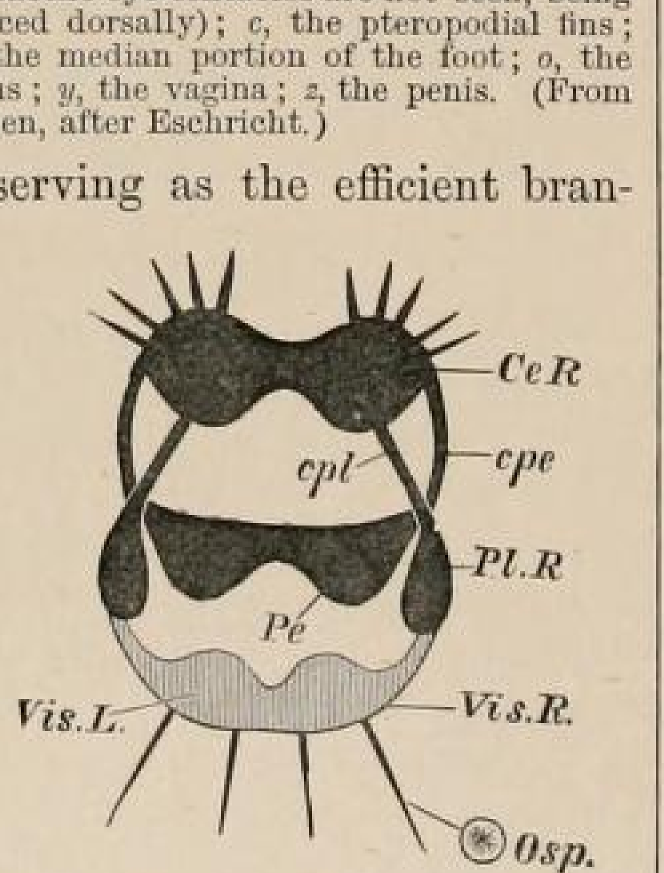


Fig. 87.—Enlarged diagram of the nerve-centres of Pneumodermon (from Spengel, after Souleyet). *CeR*, right cerebral ganglion; *Pl.R*, right pleural ganglion; *Pe*, right pedal ganglion; *Vis.R.*, right visceral ganglion; *Vis.L.*, left visceral ganglion; *cpe*, right cerebro-pedal connective; *cpl*, right cerebro-pleural connective; *Osp.*, osphradium connected by a nerve with the right visceral ganglion.

The pericardium is extended so as to form a very large sac passing among the viscera dorsal wards and sometimes containing the ovary or testis—the viscero-pericardial sac—which opens to the exterior either directly or through the nephridia. It has no connexion with the vascular system. The nephridia are always paired sacs, the walls of which invest the branchial advehent vessels (figs. 104, 108). They open each by a pore into the viscero-pericardial sac except in Nautilus. The anal aperture is median and raised on a papilla. Jaws (fig. 88, *e*) and a lingual ribbon (fig. 107) are well developed. The jaws have the form of a pair of powerful beaks, either horny or calcified (Nautilus), and are capable of inflicting severe wounds.

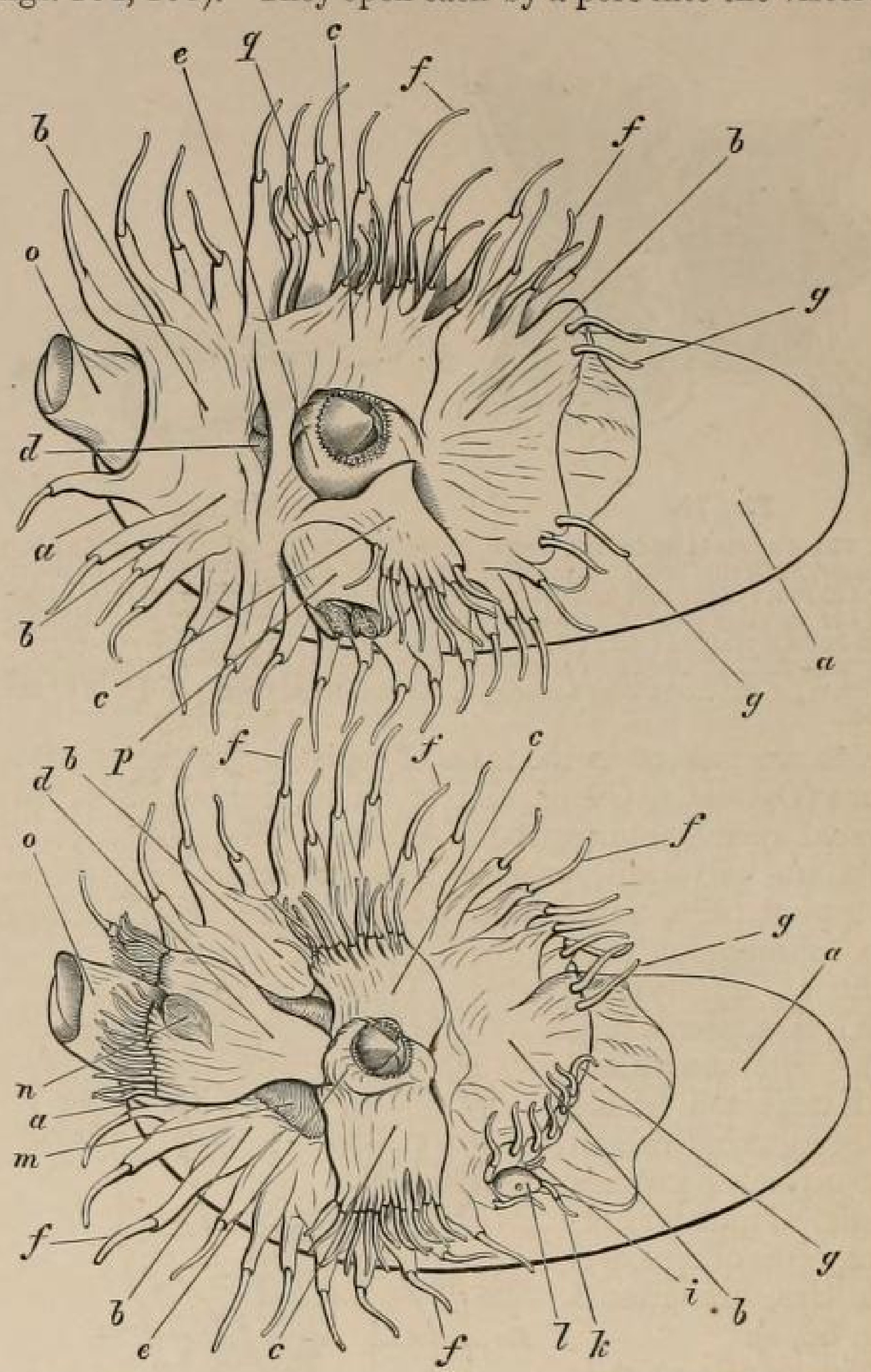


Fig. 88.—Male (upper) and female (lower) specimens of *Nautilus pompilius* as seen in the expanded condition, the observer looking down on to the buccal cone *e*; one-third the natural size linear. The drawings have been made from actual specimens by A. G. Bourne, B.Sc., and serve to show the natural disposition of the tentaculiferous lobes and tentacles of the circum-oral portion of the foot in the living state, as well as the great differences between the two sexes. *a*, the shell; *b*, the *outer* ring-like expansion (annular lobe) of the circum-oral muscular mass of the fore-foot, carrying nineteen tentacles on each side—posteriorly this is enlarged to form the "hood" (marked *v* in fig. 89 and *m.* in figs. 90 and 91), giving off the pair of tentacles marked *g* in the present figure; *c*, the right and left inner lobes of the fore-foot, each carrying twelve tentacles in the female, in the male subdivided into *p*, the "spadix" or hectocotylus on the left side, and *q*, the "anti-spadix," a group of four tentacles on the right side,—it is thus seen that the subdivided right and left inner lobes of the male correspond to the undivided right and left inner lobes of the female; *d*, the inner inferior lobe of the fore-foot, a bilateral structure in the female carrying two groups, each of fourteen tentacles, separated from one another by a lamellated organ *n*, supposed to be olfactory in function—in the male the inner inferior lobe of the fore-foot is very much reduced, and has the form of a paired group of lamellæ (*d* in the upper figure); *e*, the buccal cone, rising from the centre of the three inner lobes, and fringing the protruded calcareous beaks or jaws with a series of minute papillæ; *f*, the tentacles of the outer circum-oral lobe or annular lobe of the fore-foot projecting from their sheaths; *g*, the two most posterior tentacles of this series belonging to that part of the annular lobe which forms the hood (*m.* in figs. 90 and 91); *i*, superior ophthalmic tentacle; *k*, inferior ophthalmic tentacle; *l*, eye; *m*, paired laminated organ on each side of the base of the inner inferior lobe (*d*) of the female, probably olfactory in function; *n*, olfactory lamellæ upon the inner inferior lobe (in the female); *o*, the siphon (mid-foot); *p*, the spadix (in the male), the hectocotylized portion of the left inner lobe of the fore-foot representing four modified tentacles, eight being left unmodified; *q*, the anti-spadix (in the male), being four of the twelve tentacles of the right inner lobe of the fore-foot isolated from the remaining eight, and representing on the right side the differentiated spadix of the left side. The four tentacles of the anti-spadix are set, three on one base and one on a separate base.

There are thus in the female, where they are most numerous, ninety-four tentacles, thirty-eight on the outer annular lobe, four ophthalmic (a pair to each eye), twelve on each of the right and left inner lobes, and twenty-eight on the inner inferior lobe.

Sense-organs are highly developed; the eye exhibits a very special elaboration of structure in the Dibranchiata, and a remarkable archaic form in the Nautilus. Otocysts are present in all. The typical osphradium is not present, except in Nautilus, but other organs are present in the cephalic region, to which an olfactory function is ascribed both in Nautilus and in the other Siphonopoda.

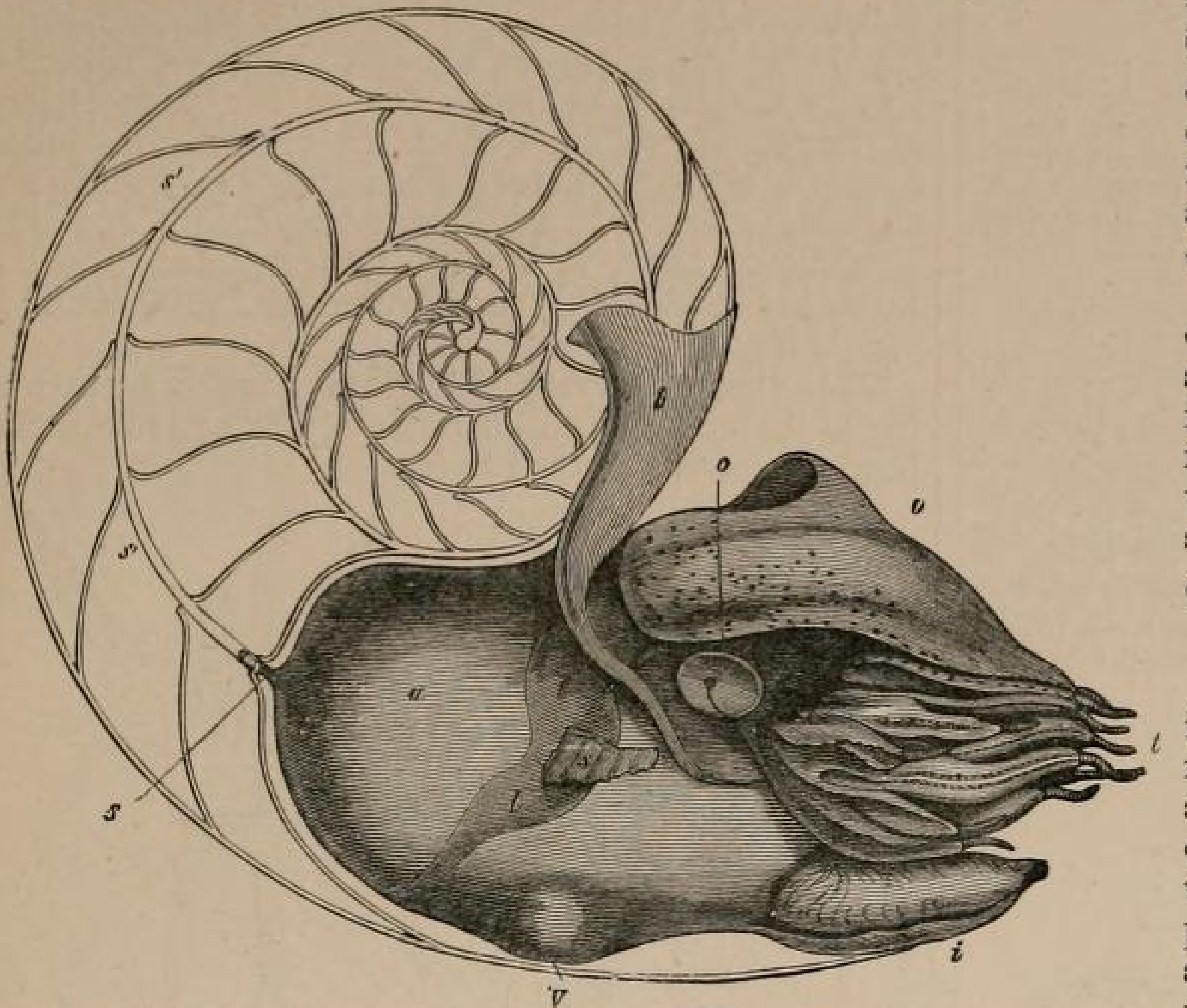


FIG. 89.—Lateral view of the female Pearly Nautilus, contracted by spirit and lying in its shell, the right half of which is cut away (from Gegenbaur, after Owen). *a*, visceral hump; *b*, portion of the free edge of the mantle-skirt reflected on to the shell,—the edge of the mantle-skirt can be traced downwards and forwards around the base of the mid-foot or siphon *i*; *l*, *l*, superficial origin of the retractor muscle of the mid-foot (siphon), more or less firmly attached to the shell, of which a small piece (*s*) is seen between the letters *l*, *l*; *s* (farther back) points to the siphuncular pedicle, which is broken off short and not continued, as in the perfect state, through the whole length of the siphuncle of the shell, also marked *s* and *s′*; *o* points to the right eye; *t* is placed near the extremities of the contracted tentacles of the outer or annular lobe of the fore-foot,—the jointed tentacles are seen protruding a little from their long cylindrical sheaths; *v*, the dorsal "hood" formed by an enlargement in this region of the annular lobe of the fore-foot (*m*. in figs. 90, 91); *V*, a swelling of the mantle-skirt, indicating the position on its inner face of the nidamental gland (see fig. 101, *g.n.*).

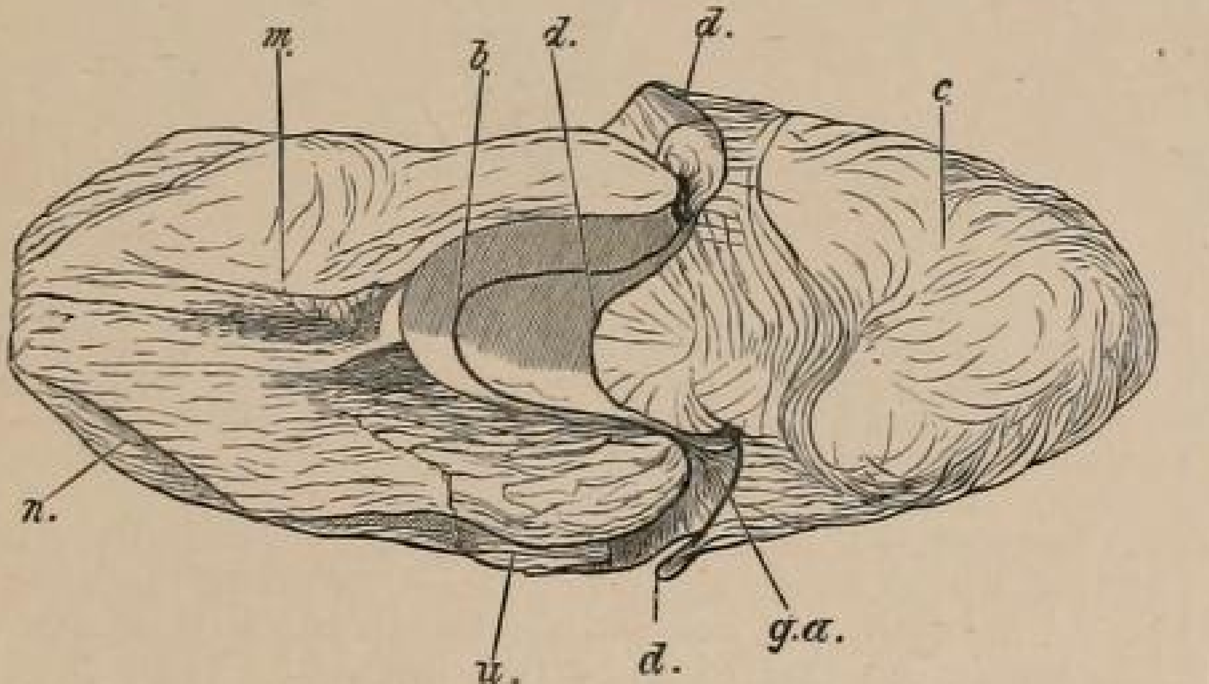


FIG. 90.—Spirit specimen of female Pearly Nautilus, removed from its shell, and seen from the antero-dorsal aspect (drawn from nature by A. G. Bourne). *m*., the dorsal "hood" formed by the enlargement of the outer or annular lobe of the fore-foot, and corresponding to the sheaths of two tentacles (*g*, *g* in fig. 88); *n*., tentacular sheaths of lateral portion of the annular lobe; *u*., the left eye; *b*., the nuchal plate, continuous at its right and left posterior angles with the root of the mid-foot, and corresponding to the nuchal cartilage of Sepia; *c*., visceral hump; *d*., the free margin of the mantle-skirt, the middle letter *d*. points to that portion of the mantle-skirt which is reflected over a part of the shell as seen in fig. 89, *b*; the cup-like fossa to which *b*. and *d*. point in the present figure is occupied by the coil of the shell; *g.a.* points to the lateral continuation of the nuchal plate *b*. to join the root of the mid-foot or siphon.

The gonads are always separated in male and female individuals. The genital aperture and duct is sometimes single, when it is the left; sometimes the typical pair is developed right and left of the anus. The males of nearly all Siphonopoda have been shown to be characterized by a peculiar modification of the arm-like processes or lobes of the fore-foot, connected with the copulative function. The term hectocotylization is applied to this modification (see figs. 88, 95, 96). Elaborate spermatophores or sperm-ropes are formed by all Siphonopoda, and very usually the female possesses special capsule-forming and nidamental glands for providing envelopes to the eggs (fig. 101, *g.n.*). The egg of all Siphonopoda is large, and the development is much modified by the presence of an excessive amount of food-material diffused in the protoplasm of the egg-cell. Trochosphere and veliger stages of development are consequently not recognizable.

The Siphonopoda are divisible into two orders, the names of which (due to Owen) describe the number of gill-plumes present; but in fact there are several characters of as great importance as those derived from the gills by which the members of these two orders are separated from one another.

Order 1.—**Tetrabranchiata** (= Schizosiphona, Tentaculifera).

Characters.—Siphonopodous Cephalopods in which the inrolled lateral margins of the mid-foot are not fused, but form a siphon by apposition (fig. 101). The circum-oral lobes of the fore-foot carry numerous sheathed tentacles (not suckers) (fig. 88). There are two pairs of ctenidial gills (hence Tetrabranchiata), and two pairs of nephridia, consequently four nephridial apertures (fig. 101). The visceropericardial chamber opens by two independent apertures to the exterior and not into the nephridial sacs. There are two oviducts (right and left) in the female and two spermducts in the male, the left duct in both sexes being rudimentary.

A large external shell either coiled or straight is present, and is not enclosed by reflexions of the mantle-skirt, except such narrow-mouthed shells as that of Gomphoceras, which were probably enclosed by the mantle as in the Dibranch Spirula. The shell consists of a series of chambers, the last formed of which is occupied by the body of the animal, the hinder ones (successively deserted) containing gas (fig. 89).

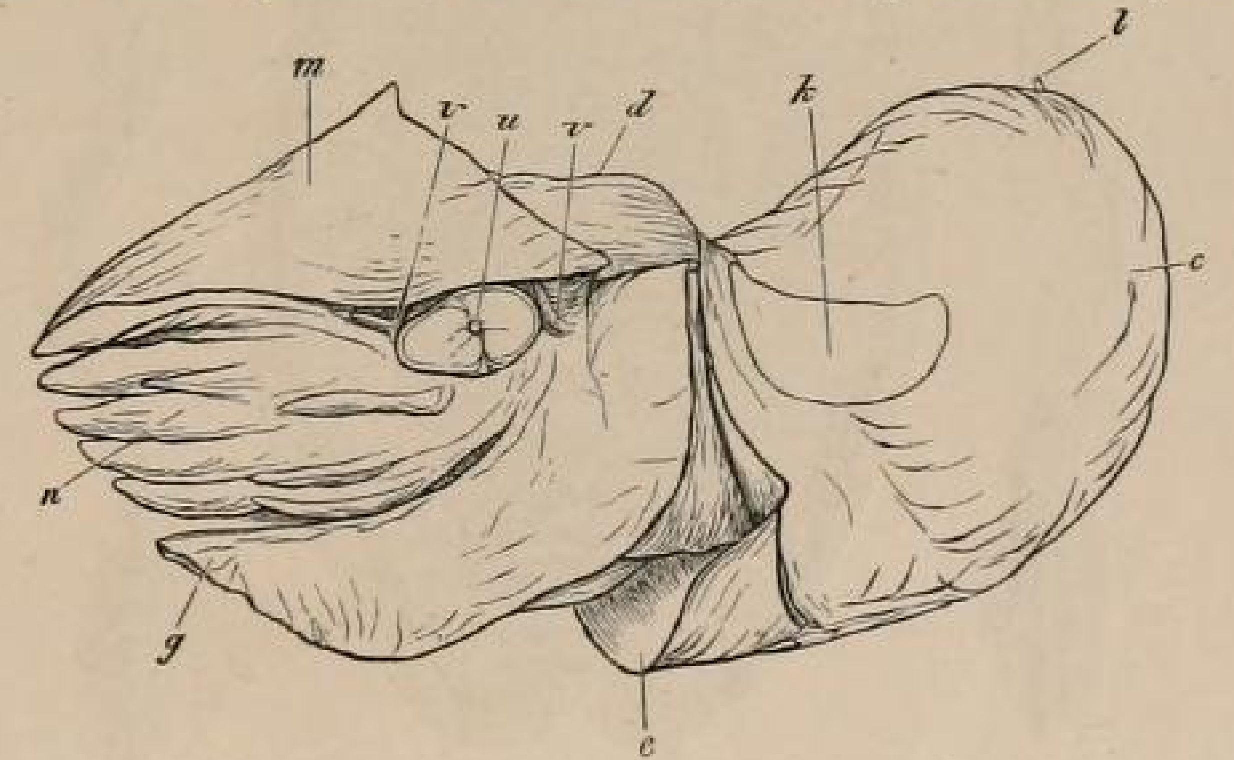


FIG. 91.—Lateral view of the same specimen as that drawn in fig. 90. Letters as in that figure with the following additions—*e* points to the concave margin of the mantle-skirt leading into the sub-pallial chamber; *g*, the mid-foot or siphon; *k*, the superficial origin of its retractor muscles closely applied to the shell and serving to hold the animal in its place; *l*, the siphuncular pedicle of the visceral hump broken off short; *v*, *v*, the superior and inferior ophthalmic tentacles.

The pair of cephalic eyes are hollow chambers (fig. 118, A) opening to the exterior by minute orifices (pinhole camera), and devoid of refractive structures. A pair of osphradia are present at the base of the gills (fig. 101, *olf*). Salivary glands are wanting. An ink-sac is *not* present. Branchial hearts are *not* developed on the branchial advehent vessels.

Family 1.—*Nautilidæ.*

Genera : [*Orthoceras*], Breyn. ; [*Cyrtoceras*], Goldfuss ; [*Gomphoceras*], Münster ; [*Phragmoceras*], Brod. ; [*Gyroceras*], Meyer ; [*Ascoceras*], Barraude ; [*Oncoceras*], Hall ; [*Lituites*], Breyn. ; [*Trochoceras*], Barraude ; *Nautilus*, L. (figs. 88, 89, 90, &c.) ; [*Clymenia*], Münst. ; [*Nothoceras*], Barraude.

Family 2.—*Ammonitidæ.*

Genera : [*Bactrites*], Sanderg. ; [*Goniatites*], de Haan ; [*Rhabdoceras*], Hauer ; [*Clydonites*], Hauer ; [*Cochloceras*], Hauer ; [*Baculina*], d'Orb. ; [*Ceratites*], de Haan ; [*Baculites*], Lam. ; [*Toxoceras*], d'Orb. ; [*Crioceras*], Leveillé ; [*Ptychoceras*], d'Orb. ; [*Hamites*], Parkinson ; [*Ancyloceras*], d'Orb. ; [*Scaphites*], Parkinson ; [*Ammonites*], Breyn. ; [*Turrilites*], Lam. ; [*Helioceras*], d'Orb. ; [*Heteroceras*], d'Orb.

N.B.—The names in brackets are those of extinct genera.

Order 2.—**Dibranchiata** (= Holosiphona, Acetabulifera).

Characters.—Siphonopodous Cephalopods in which the inflected lateral margins of the mid-foot are fused so as to form a complete tubular siphon (fig. 96, *i*). The circumoral lobes of the fore-foot carry suckers disposed upon them in rows (as in the Pteropod Pneumodermon), *not* tentacles (see figs. 92, 95, 96). There is a single pair of typical ctenidia (fig. 103) acting as gills (hence Dibranchiata), and a single pair of nephridia opening by apertures right and left of the median anus (fig. 103, *r*), and by similar internal pores into the pericardial chamber, which consequently does not open directly to the surface as in Nautilus. The oviducts are sometimes paired right and left (Octopoda), sometimes that of one side only is developed (Decapoda, except Ommastrephes). The sperm-duct is always single except, according to Keferstein, in *Eledone moschata.*

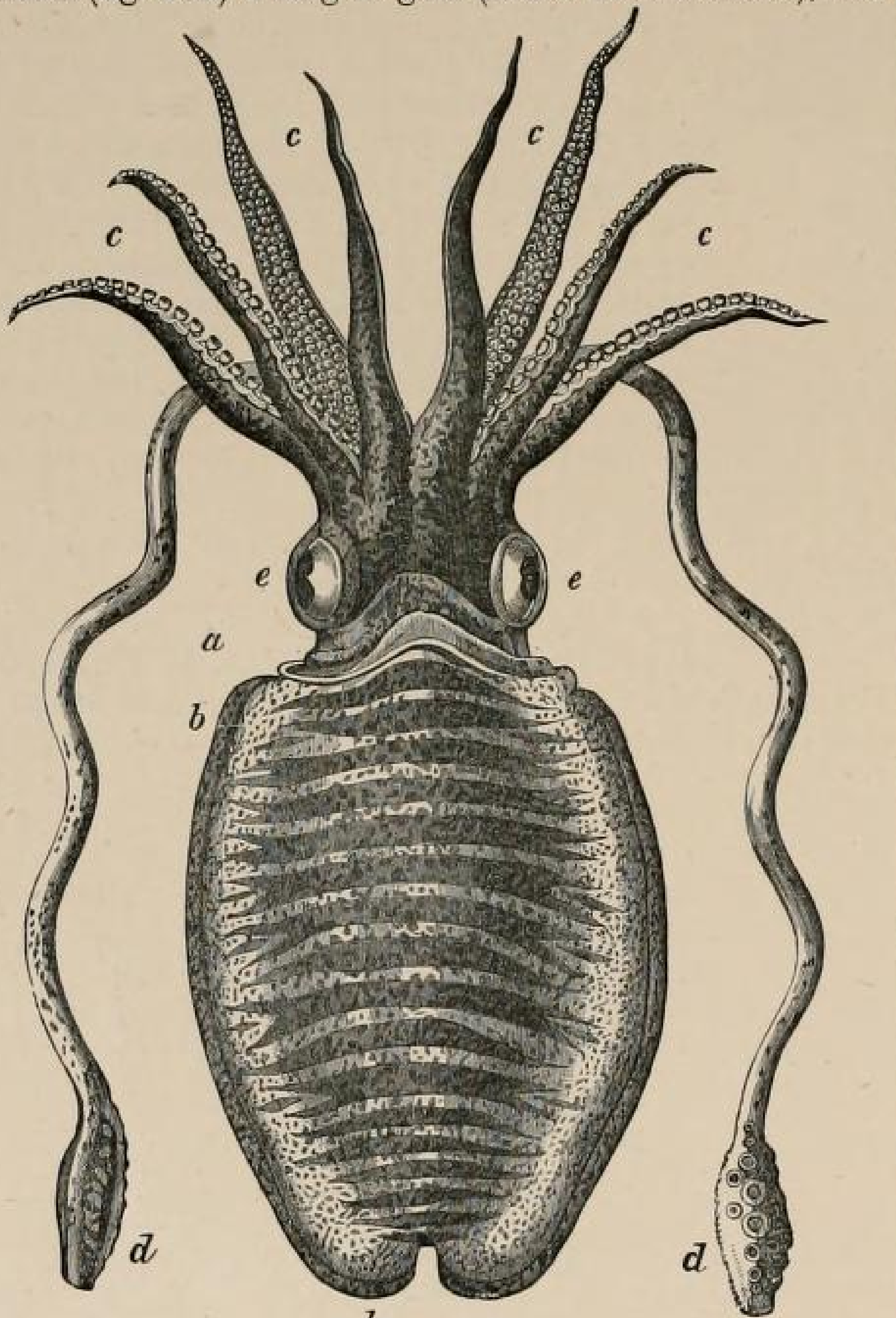


FIG. 92.—*Sepia officinalis*, L., half the natural size, as seen when dead, the long prehensile arms being withdrawn from the pouches at the side of the head, in which they are carried during life when not actually in use. *a*, neck ; *b*, lateral fin of the mantle-sac ; *c*, the eight shorter arms of the fore-foot ; *d*, the two long prehensile arms ; *e*, the eyes.

A plate-like shell is developed in a closed sac formed by the mantle (figs. 98, 99), except in the Octopoda, which have none, and in Spirula (fig. 100, D) and the extinct Belemnitidæ, which have a small chambered shell resembling that of Nautilus with or without the addition of plate-like and cylindrical accessory developments (fig. 100, C).

The pair of cephalic eyes are highly-developed vesicles with a refractive lens (fig. 120), cornea, and lid-folds,—the vesicle being in the embryo an open sac like that of Nautilus (fig. 119). Osphradia are not present, but cephalic olfactory organs are recognized. One or two pairs of large salivary glands with long ducts are present. An ink-sac formed as a diverticulum of the rectum and opening near the anus is present in all Dibranchiata (fig. 103, *t*), and has been detected even in the fossil Belemnitidæ. Branchial hearts are developed on the two branchial advehent blood-vessels (fig. 104, *vc'*, *vi*).

The Dibranchiata are divisible into two sub-orders, according to the number and character of the arm-like sucker-bearing processes of the fore-foot.

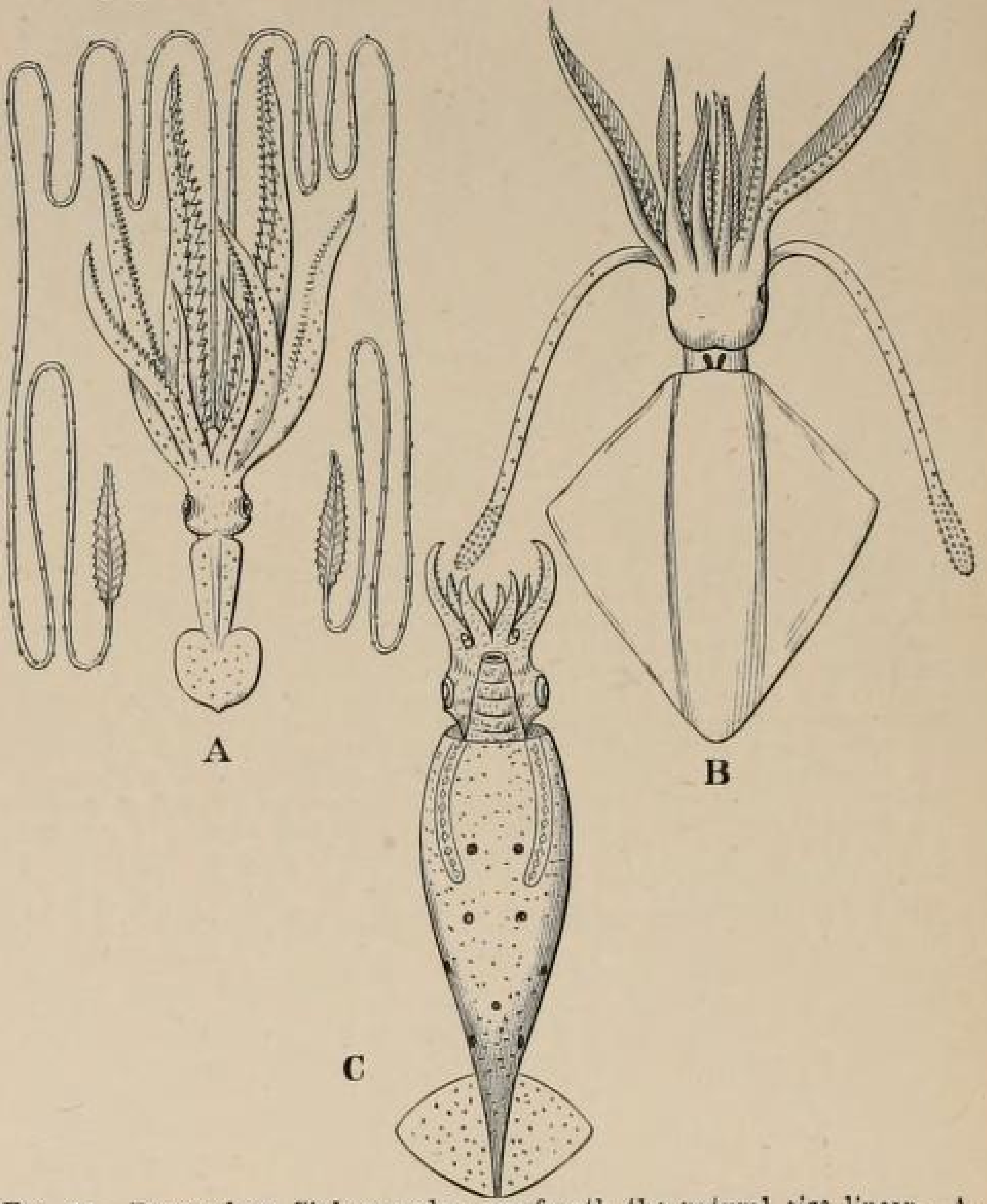


FIG. 93.—Decapodous Siphonopods ; one-fourth the natural size linear. A. *Cheiroteuthis Veranyi*, d'Orb. (from the Mediterranean). B. *Thysanoteuthis rhombus*, Troschel (from Messina). C. *Loligopsis cyclura*, Fér. and d'Orb. (from the Atlantic Ocean).

Sub-order 1.—*Decapoda.*

Characters.—Dibranchiata with the fore-foot drawn out into eight shorter and two longer arms (prehensile arms), the latter being placed right and left between the third and fourth shorter arms. The suckers are stalked and strengthened by a horny ring. The eyes are large and have a horizontal in place of a sphincter-like lid. The body is elongated and provided with lateral fins (lamelliform expansions of the mantle). The mouth has a buccal membrane. The mantle-margin is locked to the base of the siphon by a specially-developed cartilaginous apparatus. Numerous water-pores are present in the head and anterior region of the body, leading into recesses of the integument of unknown significance. The oviduct is single ; large nidamental glands are present. The viscero-pericardial space is large, and lodges the ovary (Sepia). There is always a shell present which is enclosed by the upgrowth of the mantle, so as to become "internal."

Section *a.*—*Decapoda Calciphora.*

Character.—Internal shell calcareous.

Family 1.—*Spirulidæ.*

Genus : *Spirula*, Lam. (fig. 100, D).

Family 2.—*Belemnitidæ.*

Genera : [*Spirulirostra*], d'Orb. (fig. 100, C) ; [*Beloptera*], Desh. ; [*Belemnosis*], Edw. ; [*Conoteuthis*], d'Orb. (fig. 100, A) ; [*Acanthoteuthis*], R. Wag. ; [*Belemnites*], Lister, 1678 ; [*Belemnitella*], d'Orb. ; [*Xiphoteuthis*], Huxley.

Family 3.—*Sepiadæ.*

Genera : *Sepia*, L. (figs. 92, 98, &c.) ; [*Belosepia*], Voltz ; *Coccoteuthis*, Owen.

Section *b.*—*Decapoda Chondrophora.*

Character.—Internal shell horny.

Sub-section α.—*Myopsidæ* (d'Orb.).

Eye with closed cornea, so that the surrounding water does not touch the lens; mostly frequenters of the coast.

Family 1.—*Loligidæ.*
Genera: *Loligo*, Schneid. (figs. 99, &c.); *Loliolus*, Steenstrup; *Sepioteuthis*, Blv.; [*Teuthopsis*], Desl.; [*Leptoteuthis*], Meyer; [*Belemnosepia*], Ag.; [*Beloteuthis*], Münst.
Family 2.—*Sepiolidæ.*
Genera: *Sepiola*, Schneid.; *Rossia*, Owen.

Sub-section β.—*Oigopsidæ* (d'Orb.).

Eye with open cornea, so that the surrounding water bathes the anterior surface of the lens; mostly pelagic animals.

Family 3.—*Cranchiadæ.*
Genus: *Cranchia*, Leach (fig. 94, C).
Family 4.—*Loligopsidæ.*
Genus: *Loligopsis*, Lam. (fig. 93, C).
Family 5.—*Cheiroteuthidæ.*
Genera: *Cheiroteuthis*, d'Orb. (fig. 93, A); *Histioteuthis*, d'Orb.
Family 6.—*Thysanoteuthidæ.*
Genus: *Thysanoteuthis*, Troschel (fig. 93, B).
Family 7.—*Onychoteuthidæ.*
Genera: *Gonatus*, Gray; *Onychoteuthis*, Lichtenst. (fig. 97); *Onychia*, Lesueur; *Enoploteuthis*, d'Orb., *Veranya*, Krohn; [*Plesioteuthis*], A. Wag.; [*Celæno*], Münst.; *Dosidicus*, Steenstrup; *Ommastrephes*, d'Orb.

Sub-order 2.—*Octopoda.*

Characters.—Dibranchiata with the fore-foot drawn out into eight arms only; suckers sessile, devoid of horny ring; eyes small, the outer skin can be closed over them by a sphincter-like movement. The body is short and rounded; the mantle has no cartilaginous locking apparatus, and is always fused to the head dorsally by a broad nuchal band. No buccal membrane surrounds the mouth. The siphon is devoid of valves. The oviducts are paired; there are no nidamental glands. The viscero-pericardial space is reduced to two narrow canals, passing from the nephridia to the capsule of the genital gland. There is no shell on or in the visceral hump.

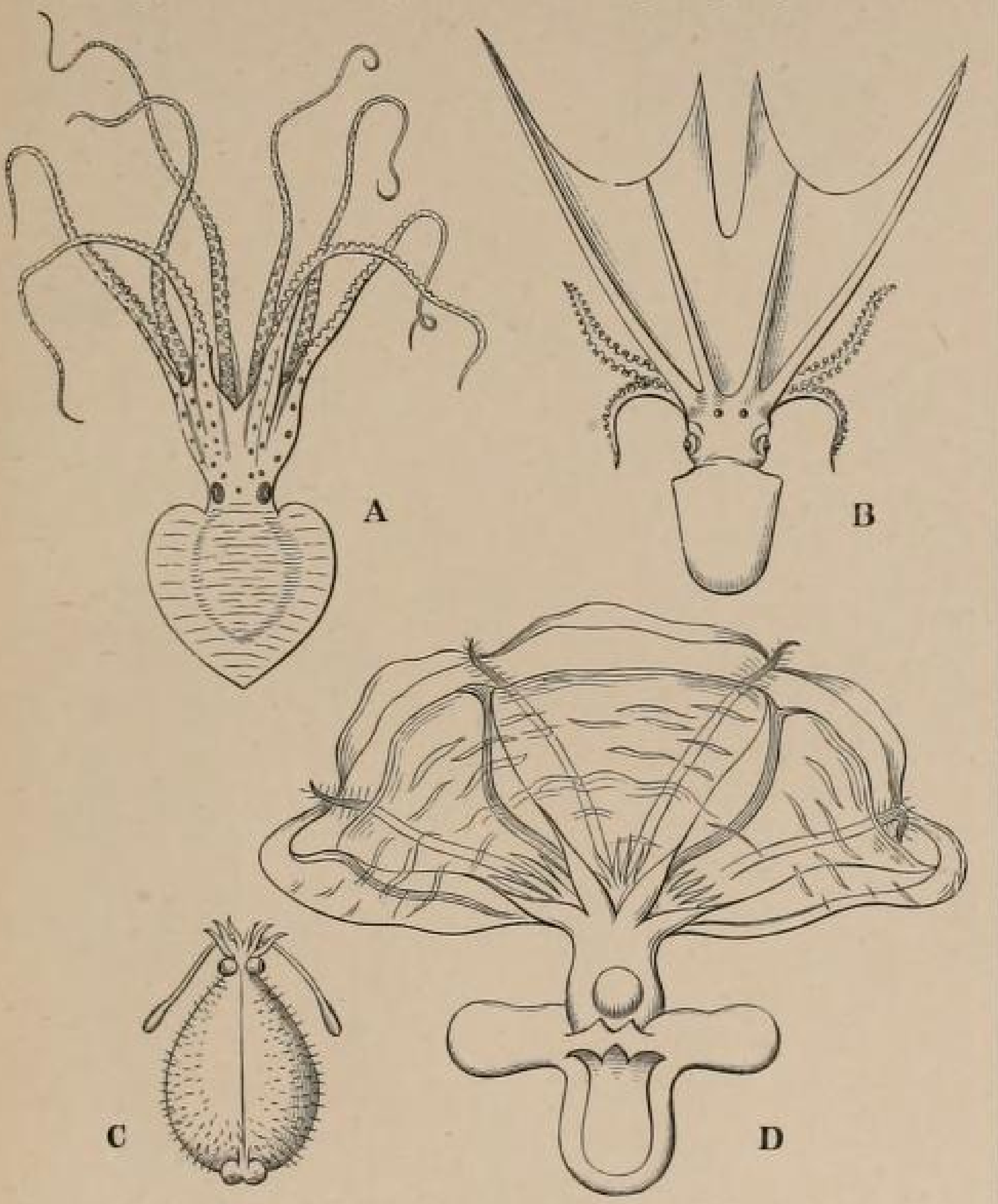


FIG. 94.—Octopodous Siphonopods; one-fourth the natural size linear. A. *Pinnoctopus cordiformis*, Quoy and Gain (from New Zealand). B. *Tremoctopus violaceus*, Ver. (from the Mediterranean). C. *Cranchia scabra*, Owen (from the Atlantic Ocean; one of the Decapoda). D. *Cirrhoteuthis Mülleri*, Esch. (from the Greenland coast).

Family 1.—*Cirrhoteuthidæ.*
Genus: *Cirrhoteuthis*, Esch. (*Sciadephorus*, Reinh.) (fig. 94, D).
Family 2.—*Octopodidæ.*
Genera: *Pinnoctopus*, d'Orb. (fig. 94, A); *Octopus*, Lam. (fig. 95); *Scæurgus*, Trosch.; *Eledone*, Leach; *Bolitæna*, Steenstrup.
Family 3.—*Philonexidæ.*
Genera: *Tremoctopus*, Delle Chiaje (*Philonexis*, d'Orb.) (fig. 94, B); *Parasira*, Steenstrup (*Octopus catenulatus*, Fér., is the female, and *Octopus carena*, Ver., is the male of the one species of this genus according to Steenstrup (fig. 96)); *Argonauta*, L. (the shell of this genus is formed only in the female by the expanded ends of the two large "arms" of the fore-foot).

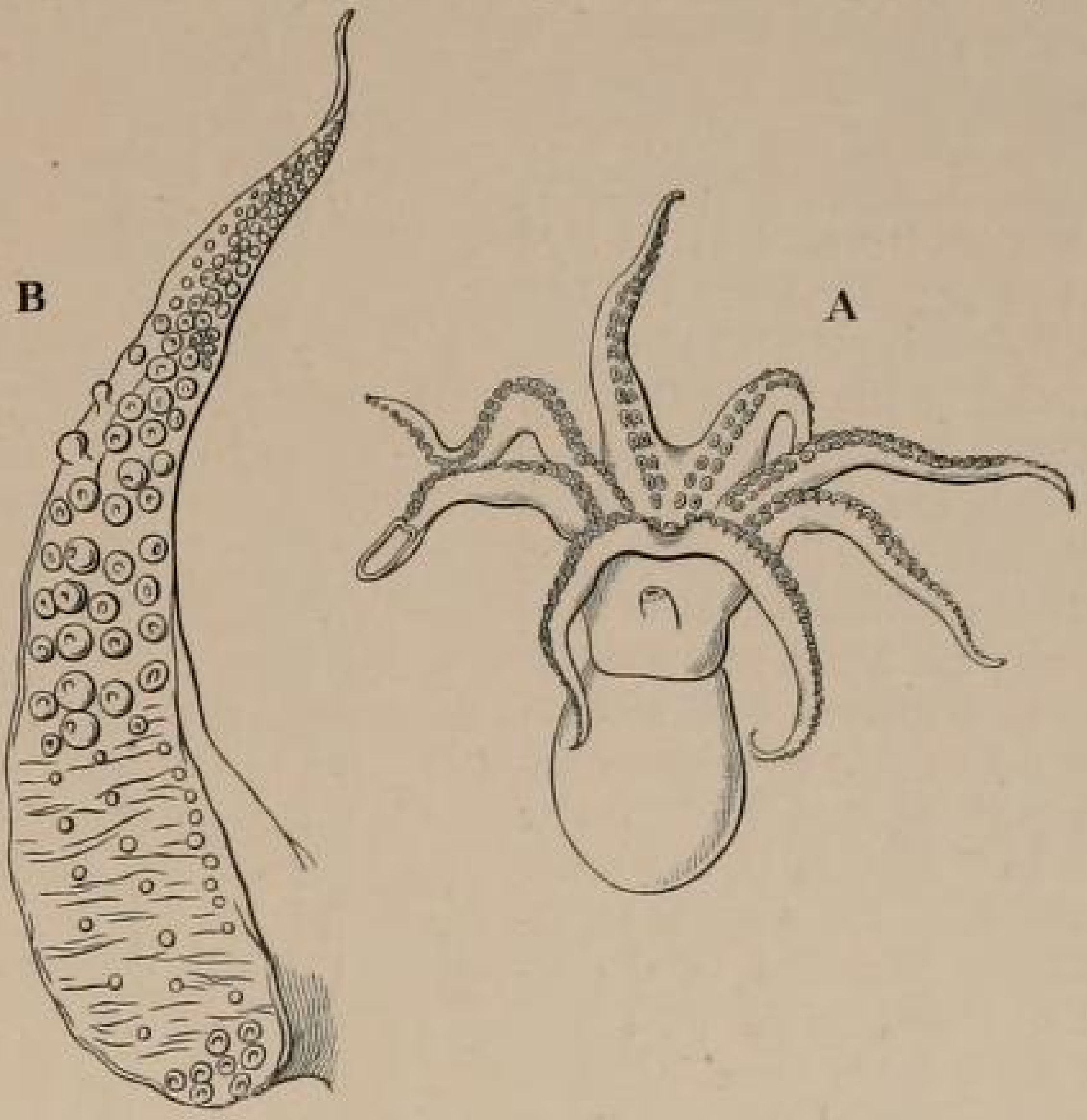


FIG. 95.—A. Male specimen of *Octopus grœnlandicus*, with the third arm of the right side hectocotylized. B. Enlarged view of the hectocotylized arm of Sepia.

Further Remarks on the Cephalopoda.—In order to give a more precise conception of the organization of the Cephalopoda in a concrete form we select the Pearly Nautilus for further description, and in passing its structure in review we shall take the opportunity of comparing here and there the peculiarities presented by that animal with those obtaining in allied forms. In the last edition of this work the Pearly Nautilus was made the subject of a detailed exposition by Professor Owen, and it has seemed accordingly appropriate that it should be somewhat fully treated on the present occasion also. The figures which illustrate the present description are (excepting fig. 89) original, and prepared from dissections (made under the direction of the writer) of a male and female *Nautilus pompilius*, lately purchased for the Museum of University College, London.

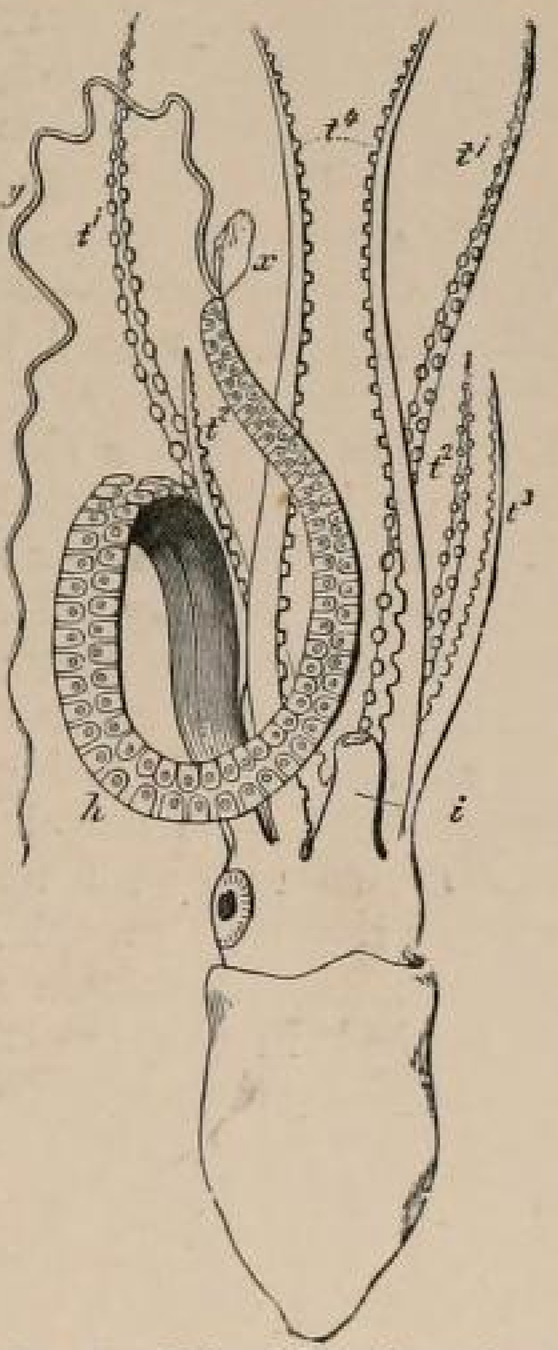


FIG. 96.—Male of *Parasira catenulata*, Steenstrup (*Octopus carena*, Ver.), showing the hectocotylized arm. t^1, t^2, t^3, t^4, the first, second, third, and fourth arms or processes of the fore-foot; *h*, the third arm of the right side hectocotylized; *x*, the apical sac of the hectocotylized arm; *y*, the filament which issues from the sac when development is complete; *i*, the siphon. (From Gegenbaur.)

Visceral Hump and Shell.—The visceral hump of Nautilus (if we exclude from consideration the fine siphuncular pedicle which it trails, as it were, behind it) is very little, if at all, affected by the coiled form of the shell which it carries, since the animal always slips forward in the shell as it grows, and inhabits a chamber which is practically cylindrical (fig. 89). Were the deserted chambers thrown off instead of being accumulated behind the inhabited chamber as a coiled series of air-chambers, we should have a more correct indication in the shell of the extent and form of the animal's body. Amongst Gastropods it is not very unusual to find the animal slipping forward in its shell as growth advances and leaving an unoccupied chamber in the apex of the shell. This may indeed become shut off from the occupied cavity by a transverse septum, and a series of such septa may be formed (fig. 42), but in no Gastropod are these apical chambers known to contain a gas during the life of the animal in whose shell they occur. A further peculiarity of the Nautilus shell and of that of the allied extinct Ammonites, Scaphites, Orthoceras, &c., and of the living Spirula, is that the series of deserted air-chambers are traversed by a cord-like pedicle extending from the centro-dorsal area of the visceral hump to the smallest and first-formed chamber of the series. No structure comparable to this siphuncular pedicle is known in any other Mollusca. Its closest representative is found in the so-called "contractile cord" of the remarkable form Rhabdopleura, referred according to present knowledge to the Polyzoa. There appears to be no doubt that the deserted chambers of the Nautilus shell contain in the healthy living animal a gas which serves to lessen the specific gravity of the whole organism. The gas is said to be of the same composition as the atmosphere, with a larger proportion of nitrogen. With regard to its origin we have only conjectures. Each septum shutting off an air-containing chamber is formed during a period of quiescence, probably after the reproductive act, when the visceral mass of the Nautilus may be slightly shrunk, and gas is secreted from the dorsal integument so as to fill up the space previously occupied by the animal. A certain stage is reached in the growth of the animal when no new chambers are formed. The whole process of the loosening of the animal in its chamber and of its slipping forward when a new septum is formed, as well as the mode in which the air-chambers may be used as a hydrostatic apparatus, and the relation to this use, if any, of the siphuncular pedicle, is involved in obscurity, and is the subject of much ingenious speculation. In connexion with the secretion of gas by the animal, besides the parallel cases ranging from the Protozoon Arcella to the Physoclistic Fishes, from the Hydroid Siphonophora to the insect-larva Corethra, we have the identical phenomenon observed in the closely-allied Sepia when recently hatched. Here, in the pores of the internal rudimentary shell, gas is observable, which has necessarily been liberated by the tissues which secrete the shell, and not derived from any external source (Huxley).

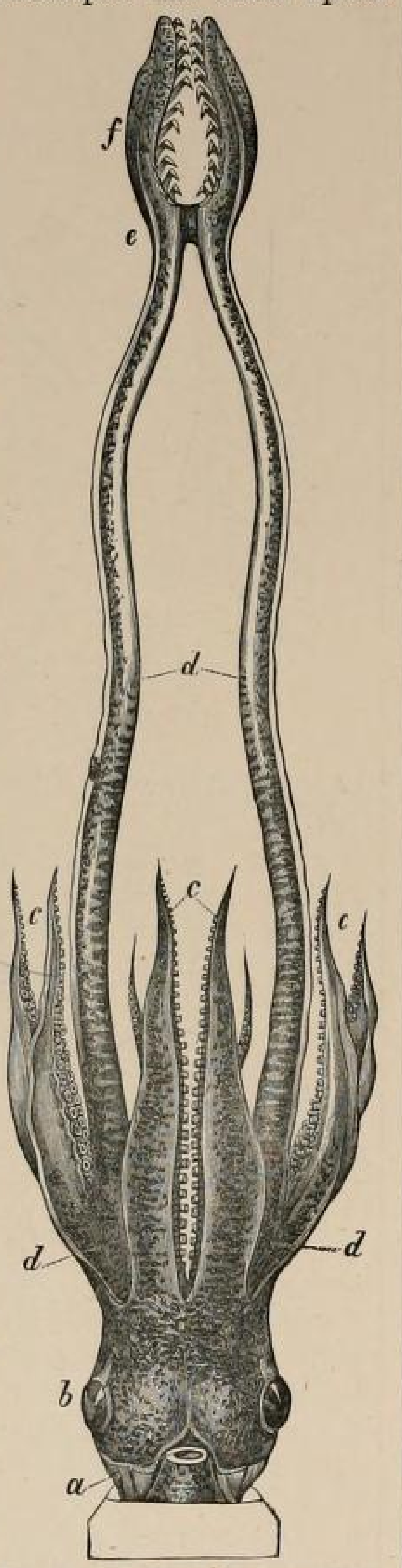


FIG. 97.—Head and circum-oral processes of the fore-foot of Onychoteuthis (from Owen). *a*, neck; *b*, eye; *c*, the eight short arms; *d*, long prehensile arms, the clavate extremities of which are provided with suckers at *e*, and with a double row of hooks beyond at *f*. The temporary conjunction of the arms by means of the suckers enables them to act in combination.

The coiled shell of Nautilus, and by analogy that of the Ammonites, is peculiar in its relation to the body of the animal, inasmuch as the curvature of the coil proceeding from the centro-dorsal area is towards the head or forward, instead of away from the head and backwards as in other discoid coiled shells such as Planorbis; the coil is in fact absolutely reversed in the two cases. Amongst the extinct allies of the Nautilus (Tetrabranchiata) we find shells of a variety of shapes, open coils such as Scaphites, leading on to perfectly cylindrical shells with chamber succeeding chamber in a straight line (Orthoceras), whence again we may pass to the cork-screw spires formed by the shell of Turrilites.

Whilst the Tetrabranchiata, so far as we can recognize their remains, are characterized by these large chambered shells, which, as in Nautilus, were with the exception of some narrow-mouthed forms such as Gomphoceras but very partially covered by reflexions of the mantle-skirt (fig. 89, *b*), the Dibranchiata present an interesting series of gradations, in which we trace—(*a*) the diminution in relative size of the chambered shell; (*b*) its complete investiture by reflected folds of the mantle (Spirula, fig. 100, D); (*c*) the concrescence

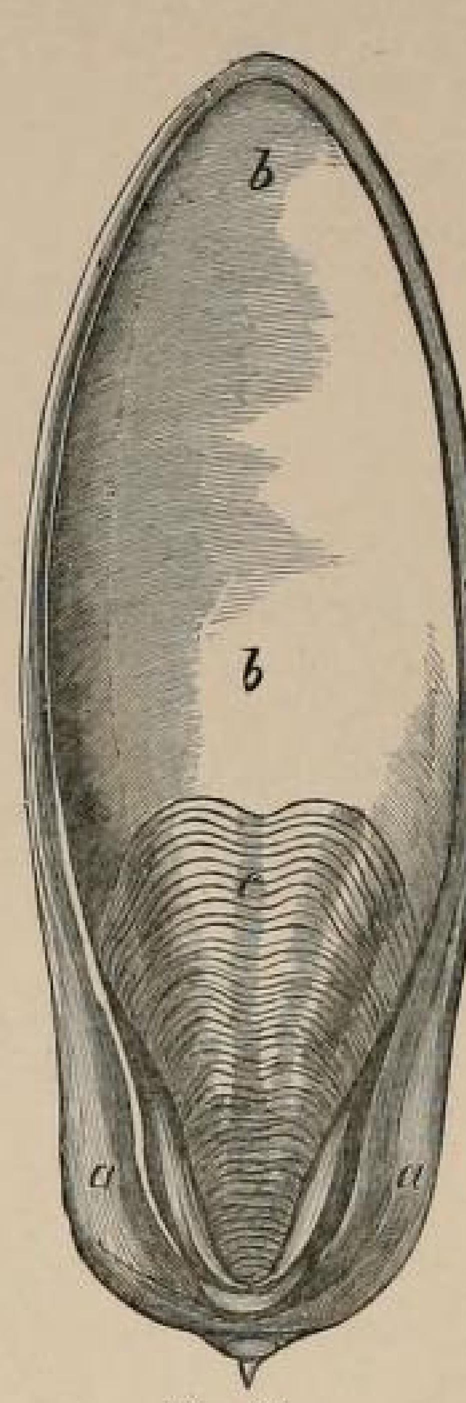


Fig. 98.

Fig. 99.

FIG. 98.—The calcareous internal shell of *Sepia officinalis*, the so-called cuttle-bone. *a*, lateral expansion; *b*, anterior cancellated region; *c*, laminated region, the laminæ enclosing air.
FIG. 99.—The horny internal shell or gladius or pen of Loligo.

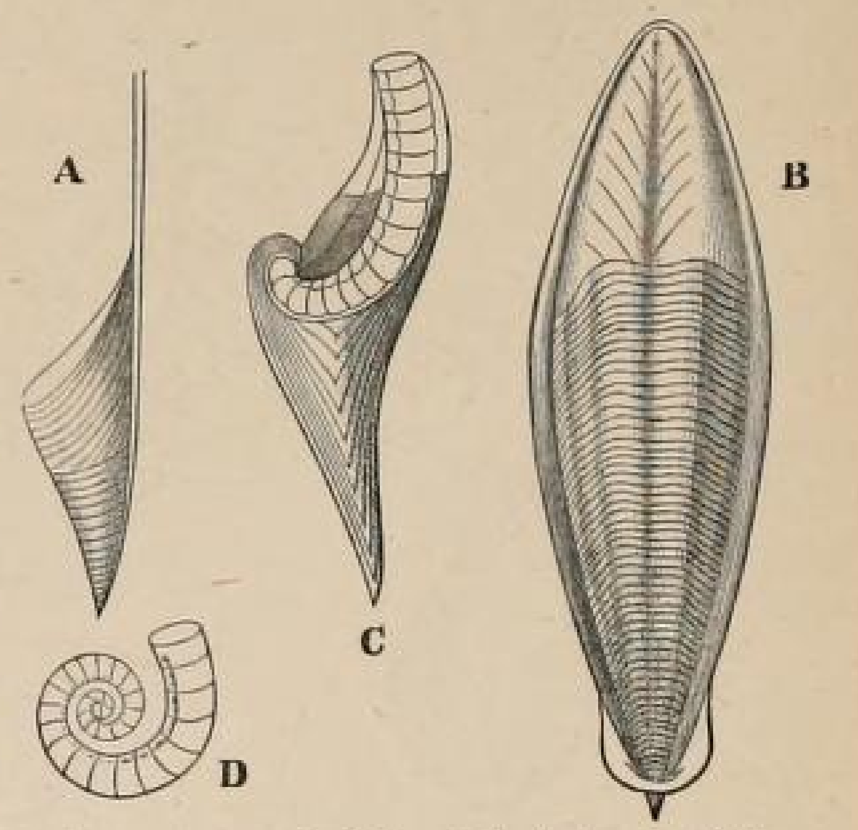


FIG. 100.—Internal shells of Cephalopoda Siphonopoda. A. Shell of *Conoteuthis dupiniana*, d'Orb. (from the Neocomian of France). B. Shell of *Sepia orbigniana*, Fér. (Mediterranean). C. Shell of *Spirulirostra Bellardii*, d'Orb. (from the Miocene of Turin). The specimen is cut so as to show in section the chambered shell and the laminated "guard" deposited upon its surface. D. Shell of *Spirula lævis*, Gray (New Zealand).

of the folds of the mantle to form a definitely-closed shell-sac; (*d*) the secretion by these mantle-folds or walls of the shell-sac of additional laminæ of calcareous shell-substance, which invest the original shell and completely alter its appearance (Spirulirostra, fig. 100, C; Belemnites); (*e*) the gradual dwindling and total disappearance of the original chambered shell, and survival alone of the calcareous laminæ deposited by the inner walls of the sac (Sepia, fig. 100, B); (*f*) the disappearance of all calcareous substance from the pen or plate which now represents the contents of the shell-sac, and its persistence as a horny body simply (Loligo, fig. 99); (*g*) the total disappearance of the shell-sac itself, and consequently of its pen or plate, nevertheless the rudiments of the shell-sac appearing in the embryo and then evanescing (Octopus). The early appearance of the sac of the mantle in which the shell is enclosed, in Dibranchiata, has led to an erroneous identification of this sac with the primitive shell-sac of the archi-Mollusc (fig. 1), of Chiton (fig. 10, A), of Arion (fig. 69, D, *a*), and of the normally-developing Molluscan embryo (figs. 68 and 72***, *sh*). The first appearance of the shell-sac of Dibranchiata is seen in figs. 121 and 122, its formation as an open upgrowth of the centro-dorsal area of the embryo having been demonstrated by Lankester (**34**) in 1873, who subsequently showed (**35**) that the same shell-sac appears and disappears without closing up in Argonauta and Octopus, and pointed out the distinctness of this sac and the primitive shell-gland. The shell of the female Argonauta is not formed by the visceral hump, but by the enlarged arms of the foot, which are in life always closely applied to it.

The shell of such Pteropoda as have shells (the Thecosomata) is excessively light, and fits close to the animal, no air-chambers being formed. It is important to note that in this division of the Cephalopoda there is the same tendency, which is carried so far in the Dibranchiate Siphonopods, for the mantle-skirt to be reflected over and closely applied to the shell (*e.g.*, Cavolinia, figs. 79 and 80). But in Pteropoda there is no complete formation of a closed sac by the reflected mantle, no thickening of the enclosed shell, no dwindling of the original shell and substitution for it of a laminated plate. The variety of form of the glass-like shells of Pteropoda is a peculiarity of that group.

Head, Foot, Mantle-skirt, and Sub-pallial Chamber.—In the Pearly Nautilus the ovoid visceral hump is completely encircled by the free flap of integument known as mantle-skirt (fig. 91, *d*, *e*). In the antero-dorsal region this flap is enlarged so as to be reflected a little over the coil of the shell which rests on it. In the postero-ventral region the flap is deepest, forming an extensive sub-pallial chamber, at the entrance of which *e* is placed in fig. 91. A view of the interior of the sub-pallial chamber, as seen when the mantle-skirt is retroverted and the observer faces in the direction indicated by the reference line passing from *e* in fig. 91, is given in fig. 101. With this should be compared the similar view of the sub-pallial chamber of the Dibranchiate Sepia (fig. 103). It should be noted as a difference between Nautilus and the Dibranchiates that in the former the nidamental gland (in the female) lies on that surface of the pallial chamber formed by the dependent mantle-flap (figs. 101, *g.n.*; 89, *V*), whilst in the latter it lies on the surface formed by the body-wall; in fact in the former the base of the fold forming the mantle-skirt comprises in its area a part of what is unreflected visceral hump in the latter.

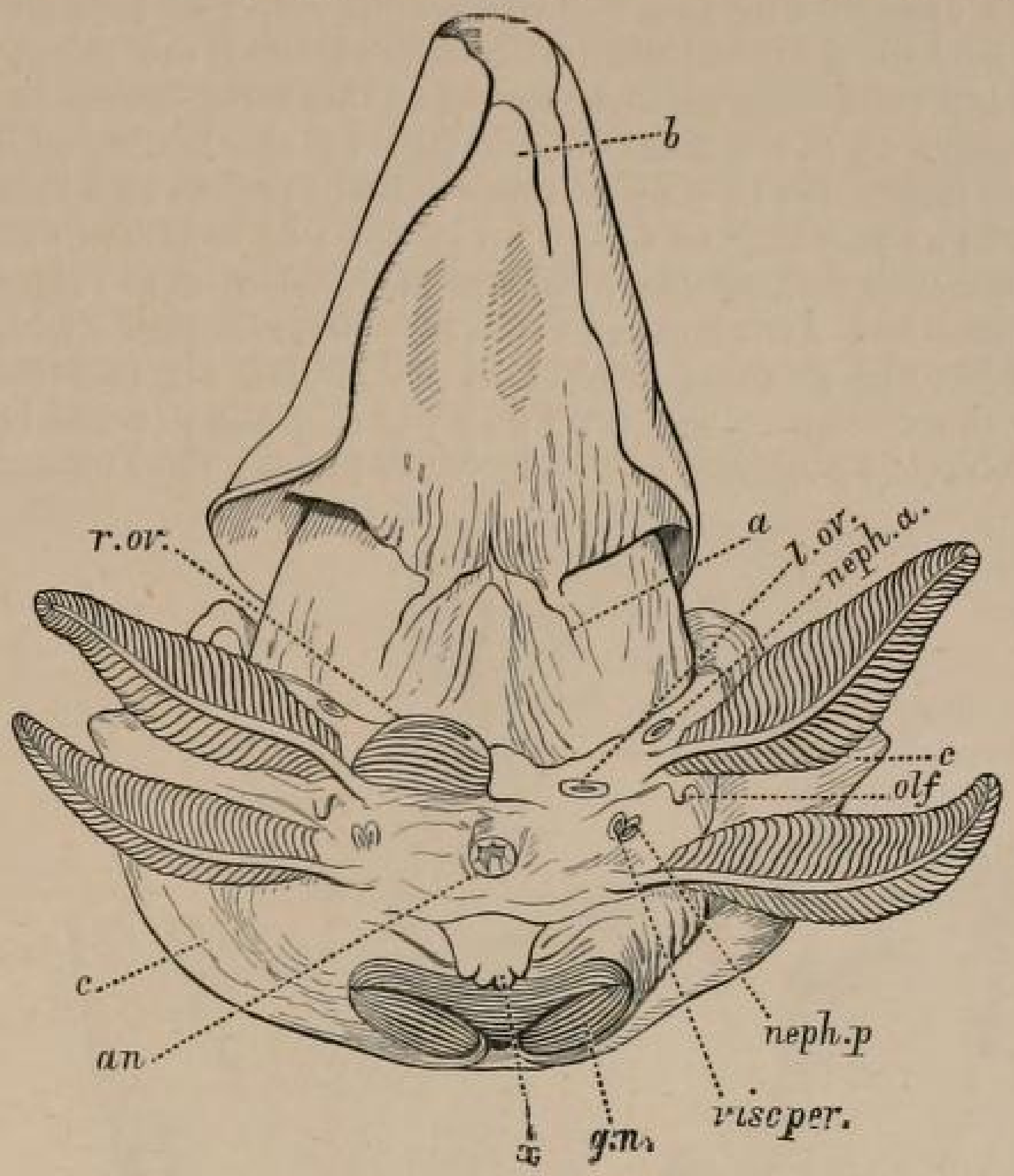


Fig. 101.—View of the postero-ventral surface of a female Pearly Nautilus, the mantle-skirt (*c*) being completely reflected so as to show the inner wall of the sub-pallial chamber (drawn from nature by A. G. Bourne). *a*, muscular band passing from the mid-foot to the integument; *b*, the valve on the surface of the funnel-like mid-foot, partially concealed by the inrolled lateral margin of the latter; *c*, the mantle-skirt retroverted; *an*, the median anus; *x*, post-anal papilla of unknown significance; *g.n.*, nidamental gland; *r.ov.*, aperture of the right oviduct; *l.ov.*, aperture of the rudimentary left oviduct (pyriform sac of Owen); *neph.a.*, aperture of the left anterior nephridium; *neph.p*, aperture of the left posterior nephridium; *viscper.*, left aperture of the viscero-pericardial sac; *olf*, the left osphradium placed near the base of the anterior gill-plume. The four gill-plumes (ctenidia) are not lettered.

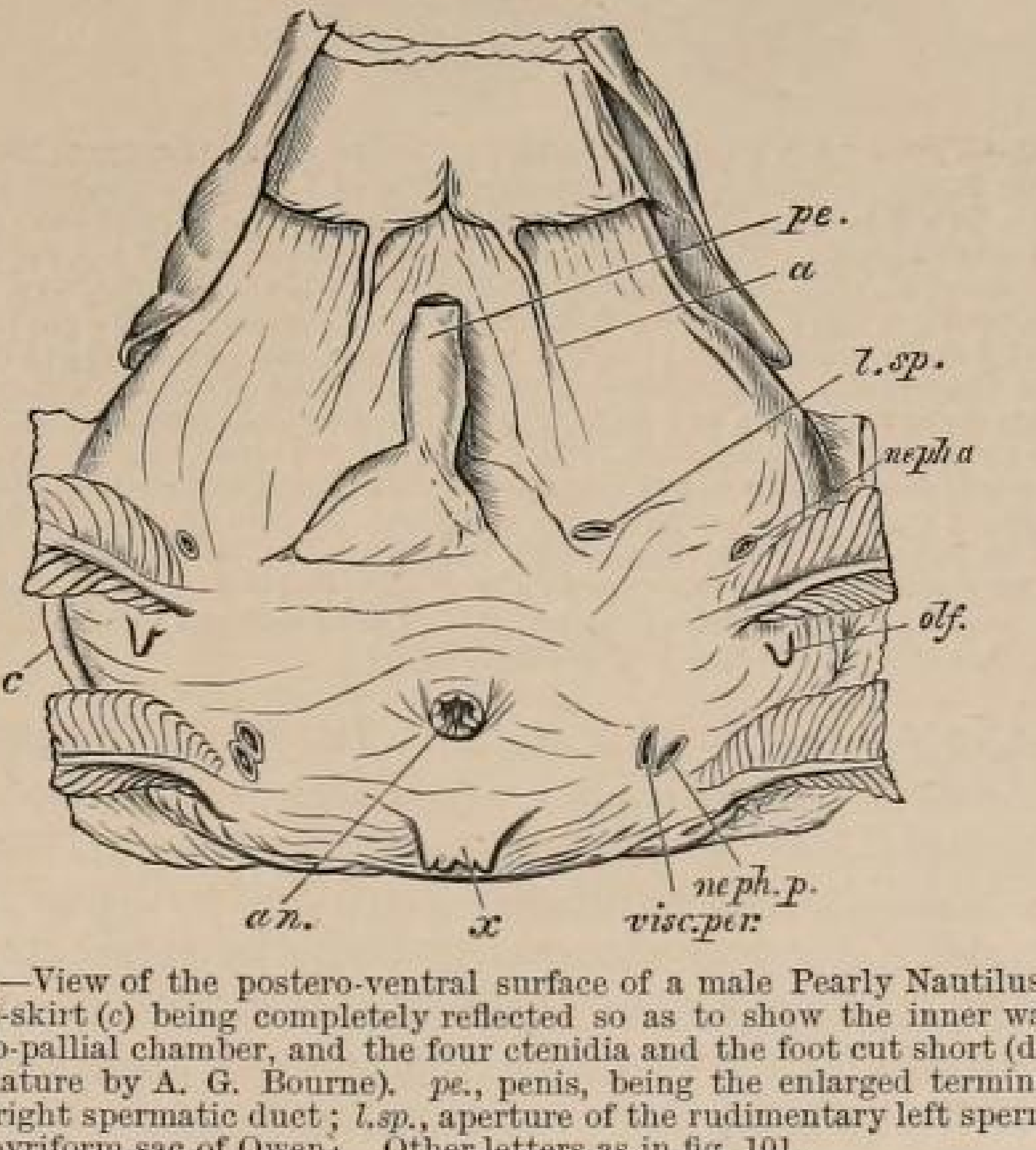


Fig. 102.—View of the postero-ventral surface of a male Pearly Nautilus, the mantle-skirt (*c*) being completely reflected so as to show the inner wall of the sub-pallial chamber, and the four ctenidia and the foot cut short (drawn from nature by A. G. Bourne). *pe.*, penis, being the enlarged termination of the right spermatic duct; *l.sp.*, aperture of the rudimentary left spermatic duct (pyriform sac of Owen). Other letters as in fig. 101.

The apertures of the two pairs of nephridia, of the viscero-pericardial sac, of the genital ducts, and of the anus are shown in position on the body-wall of the pallial chamber of Nautilus in figs. 101, 102. There are nine apertures in all, one median (the anus), and four paired. Besides these apertures we notice *two* pairs of gill-plumes which are undoubtedly typical ctenidia, and a short papilla (the osphradium) between each anterior and posterior gill-plume (see figs. 101, 102, and explanation). As compared with this in a Dibranchiate, we find (fig. 103) only four apertures, viz., the median anus with adjacent orifice of the ink-sac, the single pair of nephridial apertures, and one asymmetrical genital aperture (on the left side), except in female Octopoda and a few others where the genital ducts and their apertures are paired. No viscero-pericardial pores are present on the surface of the pallial chamber, since in the Dibranchiata the viscero-pericardial sac opens by a pore into each nephridium instead of directly to the surface. A single pair of ctenidia (gill-plumes) is present instead of the two pairs in Nautilus. The existence of two pairs of ctenidia and of two pairs of nephridia in Nautilus, placed one behind the other, is highly remarkable. The interest of this arrangement is in relation to the general morphology of the Mollusca, for it is impossible to view this repetition of organs in a linear series as anything else than an instance of metameric segmentation, comparable to the segmentation of the ringed worms and Arthropods. The only other example which we have of this metamerism in the Mollusca is presented by the Chitons. There we find not two pairs of ctenidia merely, but sixteen pairs (in some species more) accompanied by a similar metamerism of the dorsal integument, which carries eight shells. In Chiton the nephridia are not affected by the metamerism as they are in Nautilus. It is impossible on the present occasion to discuss in the way which their importance demands the significance of these two instances among Mollusca of incomplete or partial metamerism; but it would be wrong to pass them by without insisting upon the great importance which the occurrence of these isolated instances of metameric segmentation in a group of otherwise unsegmented organisms possesses, and the light which they may be made to throw upon the nature of metameric segmentation in general.

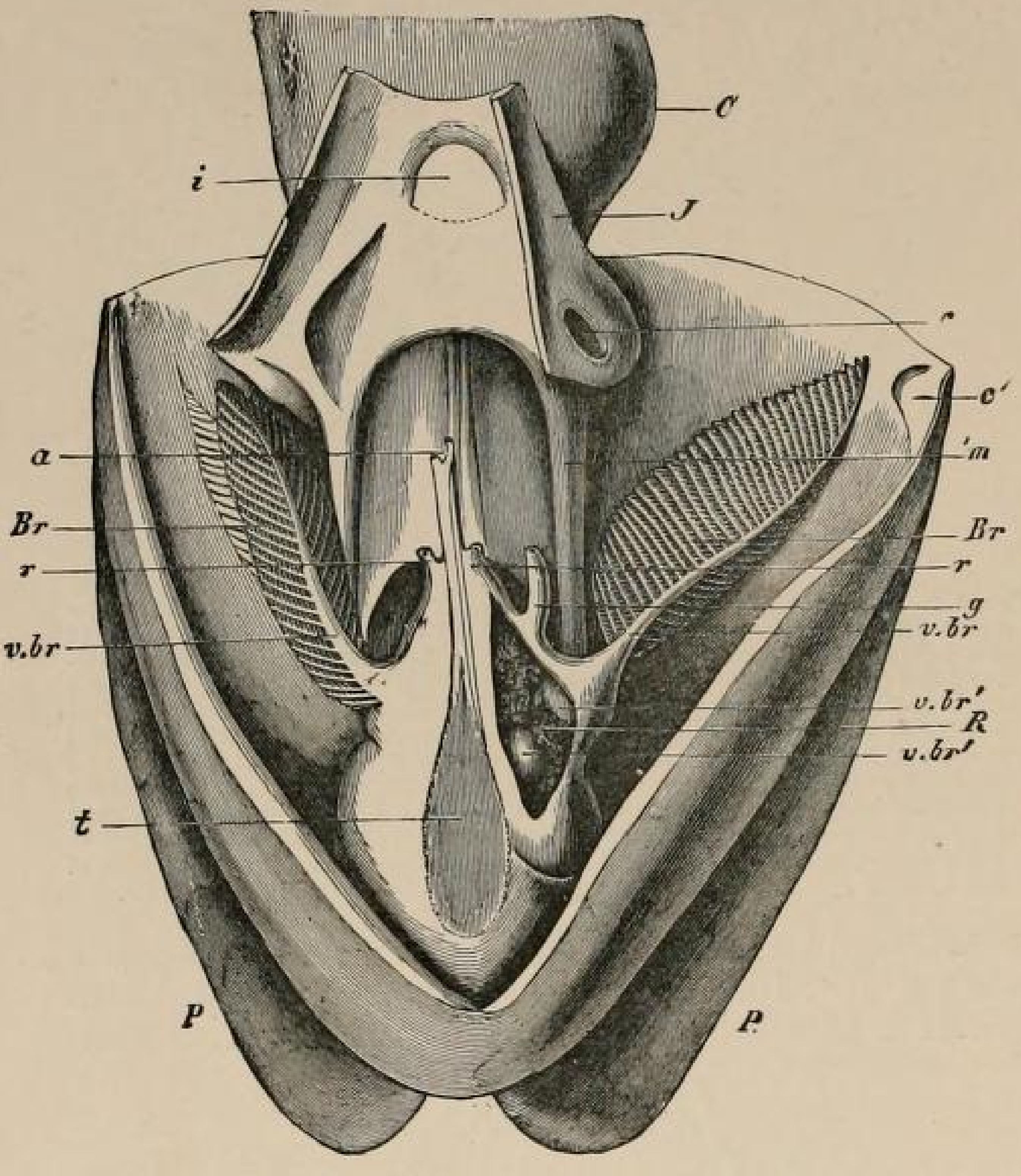


Fig. 103.—View of the postero-ventral surface of a male Sepia, obtained by cutting longitudinally the firm mantle-skirt and drawing the divided halves apart. This figure is strictly comparable with fig. 101. *C*, the head; *J*, the mid-foot or siphon, which has been cut open so as to display the valve *i*; *R*, the glandular tissue of the left nephridium or renal-sac, which has been cut open (see fig. 108); *P*, *P*, the lateral fins of the mantle-skirt; *Br*, the single pair of branchiæ (ctenidia); *a*, the anus,—immediately below it is the opening of the ink-bag; *c*, cartilaginous socket in the siphon to receive *c′*, the cartilaginous knob of the mantle-skirt,—the two constituting the "pallial hinge apparatus" characteristic of Decapoda, not found in Octopoda; *g*, the azygos genital papilla and aperture; *′i*, valve of the siphon (possibly the rudimentary hind-foot); *m*, muscular band connected with the fore-foot and mid-foot (siphon) and identical with the muscular mass *k* in fig. 91; *r*, renal papillæ, carrying the apertures of the nephridia; *v.br*, branchial efferent blood-vessel; *v.br′*, bulbous enlargements of the branchial blood-vessels (see figs. 104, 108); *t*, ink-bag. (From Gegenbaur.)

The foot and head of Nautilus are in the adult inextricably grown together, the eye being the only part belonging primarily to the head which projects from the all-embracing foot. The fore-foot or front portion of the foot in Nautilus has the form of a number of lobes carrying tentacles and completely surrounding the mouth (figs. 88, 89, 91). The mid-foot is a broad median muscular process which exhibits in the most interesting manner a curling in of its margins so as to form an incomplete siphon (fig. 101), a condition which is completed and rendered permanent in the tubular funnel, which is the form presented by the corresponding part of Dibranchiata (fig. 96). The hind-foot possibly is represented by the valvular fold on the surface of the siphon-like mid-foot. In the Pteropoda the wing-like swimming lobes (epipodia or pteropodia) correspond to the two halves of the siphon, and are much the largest element of the foot. The fore-foot surrounding the head is often quite small, but in Clione and Pneumodermon carries lobes and suckers. A hind-foot is in Pteropoda often distinctly present; it is open to doubt as to whether the corresponding region of the foot in Siphonopoda is developed at all.

The lobes of the fore-foot of Nautilus and of the other Siphonopoda require further description. It has been doubted whether these lobes were rightly referred (by Huxley) to the fore-foot, and it has been maintained by some zoologists (Grenacher, Jhering) that they are truly processes of the head. It appears to the present writer to be impossible to doubt that the lobes in question are the fore-portion of the foot when their development is examined (see fig. 121, and especially fig. 72**), further, when the fact is considered that they are innervated by the pedal ganglion, and, lastly, when the comparison of such a Siphonopod as Sepia is made with such a Pteropod as Pneumodermon in its *larval* (fig. 84) as well as in its adult condition (fig. 85). The larval Pneumodermon shows clearly that the sucker-bearing processes of that Mollusc are originally far removed from the head and close in position to the pteropodial lobes of the foot. By differential growth they gradually embrace and obliterate the head, as do the similar sucker-bearing processes of Sepia. In both cases the sucker-bearing processes are "fore-foot." The fore-foot of Nautilus completely surrounds the buccal cone (fig. 88, *e*), so as to present an appearance with its expanded tentacles similar to that of the disc of a sea-anemone (Actinia). No figure has hitherto been published exhibiting this circum-oral disc with its tentacles in natural position as when the animal is alive and swimming, the small figure of Valenciennes being deficient in detail. All the published figures represent the actual appearance of the contracted spirit-specimens. Mr A. G.

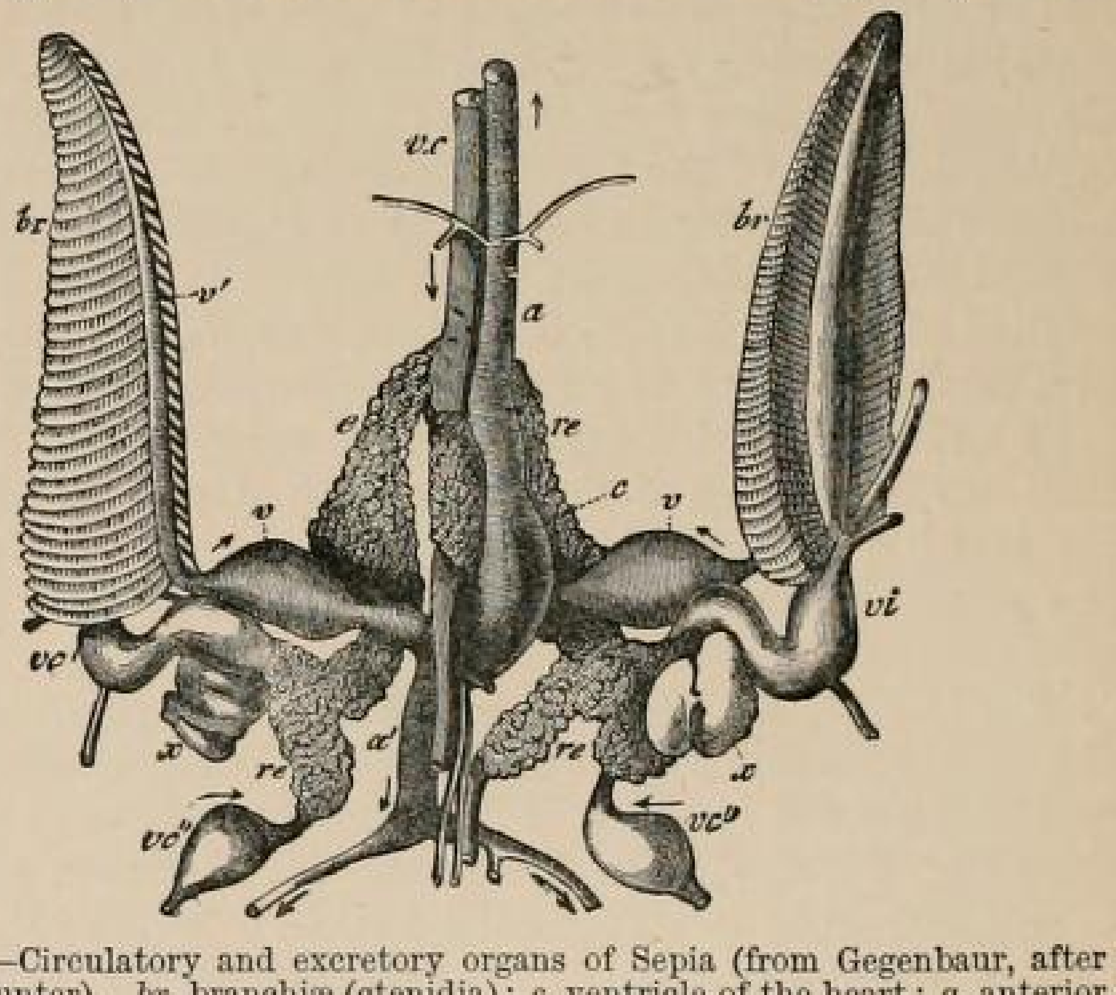


Fig. 104.—Circulatory and excretory organs of Sepia (from Gegenbaur, after John Hunter). *br*, branchiæ (ctenidia); *c*, ventricle of the heart; *a*, anterior artery (aorta); *a′*, posterior artery; *v*, the right and left auricles (enlargements of the efferent branchial veins); *v′*, efferent branchial vein on the free face of the gill-plume; *v.c*, vena cava; *vi*, *vc′*, advehent branchial vessels (branches of the vena cava, see fig. 108); *vc″*, abdominal veins; *x*, branchial hearts and appendages; *re*, *e*, glandular substance of the nephridia developed on the wall of the great veins on their way to the gills. The arrows indicate the direction of the blood-current.

Bourne, B.Sc., of University College, has prepared from actual specimens the drawings of this part in the male and female Nautilus reproduced in fig. 88, and has restored the parts to their natural form when expanded. The drawings show very strikingly the difference between male and female. In the female (lower figure), we observe in the centre of the disc the buccal cone *e* carrying the beak-like pair of jaws which project from the finely papillate buccal membrane. Three tentaculiferous lobes of the fore-foot are in immediate contact with this buccal cone; they are the right and left (*c, c*) inner lobes, as we propose to call them, and the inferior inner lobe (*d*),—called inferior because it really lies ventralwards of the mouth. This inner inferior lobe is clearly a double one, representing a right and left inner inferior lobe fused into one. A lamellated organ on its surface, probably olfactory in function (*n*), marks the separation of the constituent halves of this double lobe. Each half carries a group of fourteen tentacles. The right and the left inner lobes (*c, c*) each carry twelve tentacles. External to these three lobes the muscular substance of the mouth-embracing foot is raised into a wide ring, which becomes especially thick and large in the dorsal region where it is notably modified in form, offering a concavity into which the coil of the shell is received, and furnishing a protective roof to the retracted mass of tentacles. This part of the external annular lobe of the fore-foot is called the "hood" (figs. 90, 91, *m*.). The median antero-posterior line traversing this hood exactly corresponds to the line of concrescence of the two halves of the fore-foot, which primitively grew forward one on each side of the head, and finally fused together along this line in front of the mouth. The tentacles carried by the great annular lobe are nineteen on each side, thirty-eight in all. They are somewhat larger than the tentacles carried on the three inner lobes. The dorsalmost pair of tentacles (marked *g* in fig. 88) are the only ones which actually belong to that part of the disc which forms the great dorsal hood *m*. The hood is, in fact, to a large extent formed by the enlarged sheaths of these two tentacles. In the Ammonites (fossil Tetrabranchiata allied to Nautilus) the dorsal surface of the hood secreted a shelly plate in two pieces, known to palæontologists as Trigonellites and Aptychus. Possibly, however, this double plate was carried on the surface of the bilobed nidamental gland with the form and sculpturing of which, in Nautilus, it closely agrees. All the tentacles of the circum-oral disc are set in remarkable tubular sheaths, into which they can be drawn. The sheaths of some of those belonging to the external or annular lobe are seen in fig. 91, marked *n*. The sheaths are muscular as well as the tentacles, and are simply tubes from the base of which the solid tentacle grows. The functional significance of this sheathing arrangement is as obscure as its morphological origin. With reference to the latter, it appears highly probable that the tubular sheath represents the cup of a sucker such as is found on the fore-foot of the Dibranchiata. In any case, it seems to the writer impossible to doubt that each tentacle, and its sheath on a lobe of the circum-oral disc of Nautilus, corresponds to a sucker on such a lobe of a Dibranchiate. Keferstein follows Owen in strongly opposing this identification, and in regarding such tentacle as the equivalent of a whole lobe or arm of a Decapod or Octopod Dibranch. We find in the details of these structures, especially in the facts concerning the hectocotylus and spadix, the most conclusive reasons for dissenting from Owen's view. We have so far enumerated in the female Nautilus ninety tentacles. Four more remain which have a very peculiar position, and almost lead to the suggestion that the eye itself is a modified tentacle. These remaining tentacles are placed one above (before) and one below (behind) each eye, and bring up the total to ninety-four (fig. 91, *v, v*). They must be considered as also belonging to the fore-foot which thus surrounds the eye.

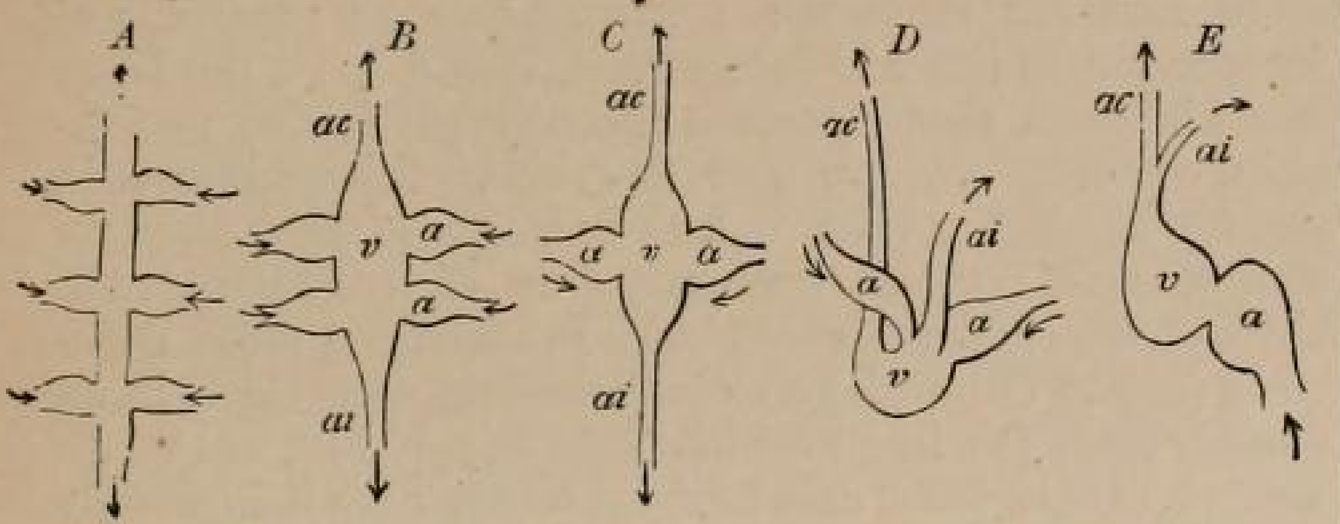


FIG. 105.—Diagram to show the relations of the heart in the Mollusca (from Gegenbaur). *A*. Part of the dorsal vascular trunk and transverse trunks of a worm. *B*. Ventricle and auricles of Nautilus. *C*. Of a Lamellibranch, of Chiton, or of Loligo. *D*. Of Octopus. *E*. Of a Gastropod. *a*, auricle; *v*, ventricle; *ac*, arteria cephalica (aorta); *ai*, arteria abdominalis. The arrows show the direction of the blood-current.

In the adult male Nautilus we find the following important differences in the tentaculiferous disc as compared with the female (see upper drawing in fig. 88). The inner inferior lobe is rudimentary, and carries no tentacles. It is represented by three groups of lamellæ (*d*), which are not fully exposed in the drawing. The right and left inner lobes are subdivided each into two portions. The right shows a larger portion carrying eight tentacles, and smaller detached groups (*q*) of four tentacles, of which three have their sheaths united whilst one stands alone. These four tentacles may be called the "anti-spadix." The left inner lobe shows a similar larger portion carrying eight tentacles, and a curious conical body in front of it corresponding to the anti-spadix. This is the "spadix" of Van der Hoeven (**36**). It carries no tentacles, but is terminated by imbricated lamellæ. These lamellæ appear to represent the four tentacles of the anti-spadix of the right internal lobe, and are generally regarded as corresponding to that modification of the sucker-bearing arms of male Dibranchiate Siphonopods to which the name "hectocotylus" is applied. The spadix is in fact the hectocotylized portion of the fore-foot of the male Nautilus. The hectocotylized arm or lobe of male Dibranchiata is connected with the process of copulation, and in the male Nautilus the spadix has probably a similar significance, though it is not possible to suggest how it acts in this relation. It is important to observe that the modification of the fore-foot in the male as compared with the female Nautilus is not confined to the existence of the spadix. The anti-spadix and the reduction of the inner inferior lobe are also male peculiarities. The external annular lobe in the male does not differ from that of the female; it carries nineteen tentacles on each side. The four ophthalmic tentacles are also present. Thus in the male Nautilus we find altogether sixty-two tentacles, the thirty-two additional tentacles of the female being represented by lamelliform structures.

If we now compare the fore-foot of the Dibranchiata with that of Nautilus, we find in the first place a more simple arrangement of its lobes, which are either four or five pairs of tapering processes (called "arms") arranged in a series around the buccal cone, and a substitution of suckers for tentacles on the surface of these lobes (figs. 92, 95, 96). The most dorsally-placed pair of arms, corresponding to the two sides of the hood of Nautilus, are in reality the most anterior (see fig. 75, (6)), and are termed the first pair. In the Octopoda there are four pairs of these arms (figs. 94, 95), in the Decapoda five pairs, of which the fourth is greatly elongated (figs. 92, 93). In Sepia and other Decapoda (not all) each of these long arms is withdrawn into a pouch beside the head, and is only ejected for the purpose of prehension. The figures referred to show some of the variations in form which these arms may assume. In the

Octopoda they are not unfrequently connected by a web, and form an efficient swimming-bell. The suckers are placed on the ad-oral surface of the arms, and may be in one, two, or four rows, and very numerous. In place of suckers in some genera we find on certain arms or parts of the arms horny hooks; in other cases a hook rises from the centre of each sucker. The hooks on the long arms of Onychoteuthis are drawn in fig. 97. The fore-foot, with its apparatus of suckers and hooks, is in the Dibranchiata essentially a prehensile apparatus, though the whole series of arms in the Octopoda serve as swimming organs, and in many (*e.g.*, the Common Octopus or Poulp) the sucker-bearing surface is used as a crawling organ.

In the males of the Dibranchiata one of the arms is more or less modified in connexion with the reproductive function, and is called the "hectocotylized arm." This name is derived from the condition assumed by the arm in those cases in which its modification is carried out to the greatest extent. These cases are those of the Octopods *Argonauta argo* and *Parasira catenulata* (fig. 96). In the males of these the third arm (on the left side in Argonauta, on the right side in Parasira) is found before the breeding season to be represented by a globular sac of integument. This sac bursts, and from it issues an arm larger than its neighbours, having a small sac at its extremity in Parasira (fig. 96, *x*), from which subsequently a long filament issues. Before copulation the male charges this arm with the spermatophores or packets of spermatozoa removed from its generative orifice beneath the mantle-skirt, and during coitus the arm becomes detached and is left adhering to the female by means of its suckers. A new arm is formed at the cicatrix before the next breeding season. The female, being much larger than the male, swims away with the detached arm lodged beneath her mantle-skirt. There, in a way which is not understood, the fertilization of the eggs is effected. Specimens of the female Parasira with the detached arm adherent were examined by Cuvier, who mistook the arm for a parasitic worm and gave to it the name Hectocotylus. Accordingly, the correspondingly modified arms of other Siphonopoda are said to be hectocotylized. Steenstrup has determined the hectocotylized condition of one or other of the arms in a number of male Dibranchs as follows:—in all, excepting Argonauta and Parasira, the modification of the arm is slight, consisting in a small enlargement of part or the whole of the arm, and the obliteration of some of its suckers, as shown in fig. 95, A, B; in Octopus and Eledone the third right arm is hectocotylized; in Rossia the first left arm is hectocotylized along its whole length, and the first right arm also in the middle only; in Sepiola only the first left arm along its whole length; in Sepia it is the fourth left arm which is modified, and at its base only; in Sepioteuthis, the same at its apex; in Loligo, the same also at its apex; in Loliolus, the same along its whole length; in Ommastrephes, Onychoteuthis, and Loligopsis no hectocotylized arm has hitherto been observed.

In the females of several Dibranchs (Sepia, &c.) the packets of spermatozoa or spermatophores received from the male have been observed adhering to the smaller arms. How they are passed in this case by the female to the ova in order to fertilize them is unknown.

Musculature, Fins, and Cartilaginous Skeleton.—Without entering into a detailed account of the musculature of Nautilus, we may point out that the great muscular masses of the fore-foot and of the mid-foot (siphon) are ultimately traceable to a large transverse mass of muscular tissue, the ends of which are visible through the integument on the right and left surfaces of the body dorsal of the free flap of the mantle-skirt (fig. 89, *l*, *l*, and fig. 91, *k*). These muscular areæ have a certain adhesion to the shell, and serve both to hold the animal in its shell and as the fixed supports for the various movements of the tentaculiferous lobes and the siphon. They are to be identified with the ring-like area of adhesion by which the foot-muscle of the Limpet is attached to the shell of that animal (see fig. 27). In the Dibranchs a similar origin of the muscular masses of the fore-foot and mid-foot from the sides of the shell—modified, as this is, in position and relations—can be traced.

In Nautilus there are no fin-like expansions of the integument, whereas such occur in the Decapod Dibranchs along the sides of the visceral hump (figs. 92, 93). As an exception among Octopoda lateral fins occur in Pinnoctopus (fig. 94, A), and in Cirrhoteuthis (fig. 94, D). In the Pteropodous division of the Cephalopoda such fin-like expansions of the dorsal integument do not occur, which is to be connected with the fact that another region, the mid-foot, which in Siphonopods is converted into a siphon, is in them expanded as a pair of fins.

In Nautilus there is a curious plate-like expansion of integument in the mid-dorsal region just behind the hood, lying between that structure and the portion of mantle-skirt which is reflected over the shell. This is shown in fig. 90, *b*. If we trace out the margin of this plate we find that it becomes continuous on each side with the sides of the siphon or mid-foot. In Sepia and other Decapods (not in Octopods) a closely similar plate exists in an exactly corresponding position (see *b* in figs. 110, 111). In Sepia a cartilaginous development occurs here immediately below the integument forming the so-called "nuchal plate," drawn in fig. 116, D. The morphological significance of this nuchal lamella, as seen both in Nautilus and in Sepia, is not obvious. Cartilage having the structure shown in fig. 117 occurs in various regions of the body of Siphonopoda. In all Glossophorous Mollusca the lingual apparatus is supported by internal skeletal pieces, having the character of cartilage; but in the Siphonopodous Cephalopoda such cartilage has a wider range.

In Nautilus a large H-shaped piece of cartilage is found forming the axis of the mid-foot or siphon (fig. 116, A, B). Its hinder part extends up into the head and supports the peri-œsophageal nerve-mass (*a*), whilst its two anterior rami extend into the tongue-like siphon. In Sepia, and Dibranchs generally, the cartilage takes a different form, as shown in fig. 116, C. The processes of this cartilage cannot be identified in any way with those of the capito-pedal cartilage of Nautilus. The lower larger portion of this cartilage in Sepia is called the cephalic cartilage, and forms a complete ring round the œsophagus; it completely invests also the ganglionic nerve-collar, so that all the nerves from the latter have to pass through foramina in the cartilage. The outer angles of this cartilage spread out on each side so as to form a cup-like receptacle for the eyes. The two processes springing right and left from this large cartilage in the median line (fig. 116, C) are the "præ-orbital cartilages;" in front of these, again, there is seen a piece like an inverted T, which forms a support to the base of the "arms" of the fore-foot, and is the "basi-brachial" cartilage. The Decapod Dibranchs have, further, the "nuchal cartilage" already mentioned, and in Sepia, a thin plate-like "sub-ostracal" or (so-called) dorsal cartilage, the anterior end of which rests on and fits into the concave nuchal cartilage. In Octopoda there is no nuchal cartilage, but two band-like "dorsal cartilages." In Decapods there are also two cartilaginous sockets on the sides of the funnel —"siphon-hinge cartilages"—into which fleshy knobs of the mantle-skirt are loosely fitted. In Sepia, along the whole base-line of each lateral fin of the mantle (fig. 92), is a "basi-pterygial cartilage." It is worthy of remark that we have, thus developed, in Dibranch Siphonopods a more complete internal cartilaginous skeleton than is to be found in some of the lower Vertebrates. There are other instances of cartilaginous endo-skeleton in groups other than the Vertebrata. Thus in some capito-branchiate Chætopods cartilage forms a skeletal support for the gill-plumes, whilst in the Arachnids (Mygale, Scorpio) and in Limulus a large internal cartilaginous plate—the ento-sternite—is developed as a support for a large series of muscles.

Alimentary Tract.—The buccal cone of Nautilus is terminated by a villous margin (buccal membrane) surrounding the pair of beak-like jaws. These are very strong and dense in Nautilus, being calcified. Fossilized beaks of Tetrabranchiata are known under the name of Rhyncholites. In Dibranchs the beaks are horny, but similar in shape to those of Nautilus. They resemble in general those of a parrot, the lower beak being the larger, and overlapping the upper or dorsal beak. The lingual ribbon and odontophoral apparatus has the structure which is typical for Glossophorous Mollusca. In fig. 107, A is represented a single row of teeth from the lingual ribbon of Nautilus, and in fig. 107, B, C, of other Siphonopoda.

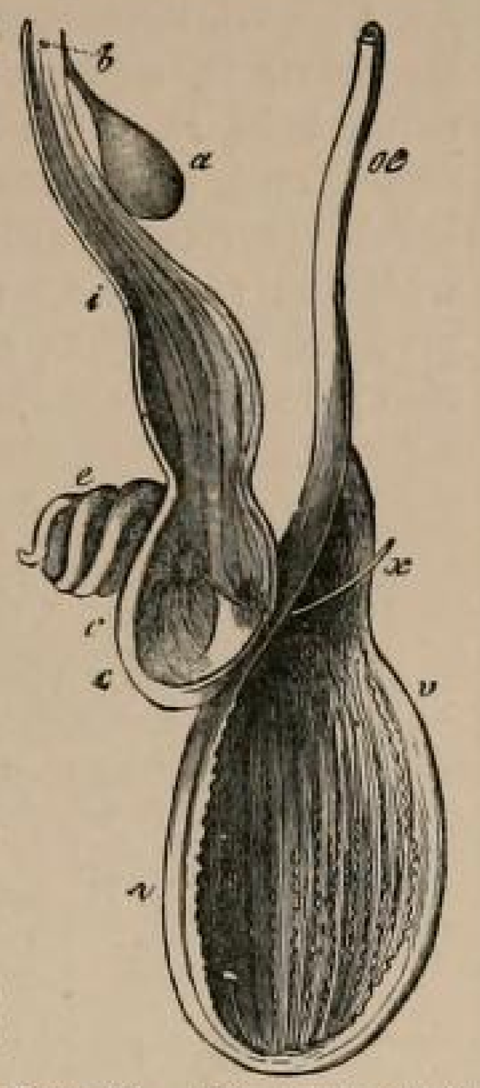


FIG. 106.—Alimentary canal of *Loligo sagittata* (from Gegenbaur). The buccal mass is omitted. *oe*, œsophagus; *v*, the stomach opened longitudinally; *x*, probe passed through the pylorus; *c*, commencement of the cæcum; *e*, its spiral portion; *i*, intestine; *a*, ink-bag; *b*, its opening into the rectum.

In Nautilus a long and wide crop or dilated œsophagus (*cr*, fig. 110) passes from the muscular buccal mass, and at the apex of the visceral hump passes into a highly muscular stomach, resembling the gizzard of a bird (*gizz*, fig. 110). A nearly straight intestine passes from the muscular stomach to the anus, near which it develops a small cæcum. In other Siphonopods the œsophagus is usually narrower (fig. 106, *oe*), and the muscular stomach more capacious (fig. 106, *v*), whilst a very important feature in the alimentary tract is formed by the cæcum. In all but Nautilus the cæcum lies near the stomach, and may be very capacious—much larger than the stomach in *Loligo vulgaris*—or elongated into a spiral coil, as in fig. 106, *e*. The simple U-shaped flexure of the alimentary tract as seen in fig. 106, and in fig. 110, is the only important one which it exhibits in the Cephalopoda,—the Pteropoda (except the Limacinida) agreeing with the Siphonopoda in this simplicity in consequence of their visceral hump being untwisted. The acini of the large liver of Nautilus are compacted into a solid reddish-brown mass by a firm membrane, as also is the case in the Dibranchiata. The liver has four paired lobes in Nautilus, which open by two bile-ducts into the alimentary canal at the commencement of the intestine. The bile-ducts unite before entering the intestine. In Dibranchiata the two large lobes of the liver are placed antero-dorsally (beneath the shell in Decapoda), and the bile-ducts open into the cæcum. Upon the bile-ducts in Dibranchiata are developed yellowish glandular diverticula, which are known as "pancreas," though neither physiologically nor morphologically is there any ground for considering either the so-called liver or the so-called pancreas as strictly equivalent to the glands so denominated in the Vertebrata. In Nautilus the equivalents of the pancreatic diverticula of the Dibranchs can be traced upon the relatively shorter bile-ducts.

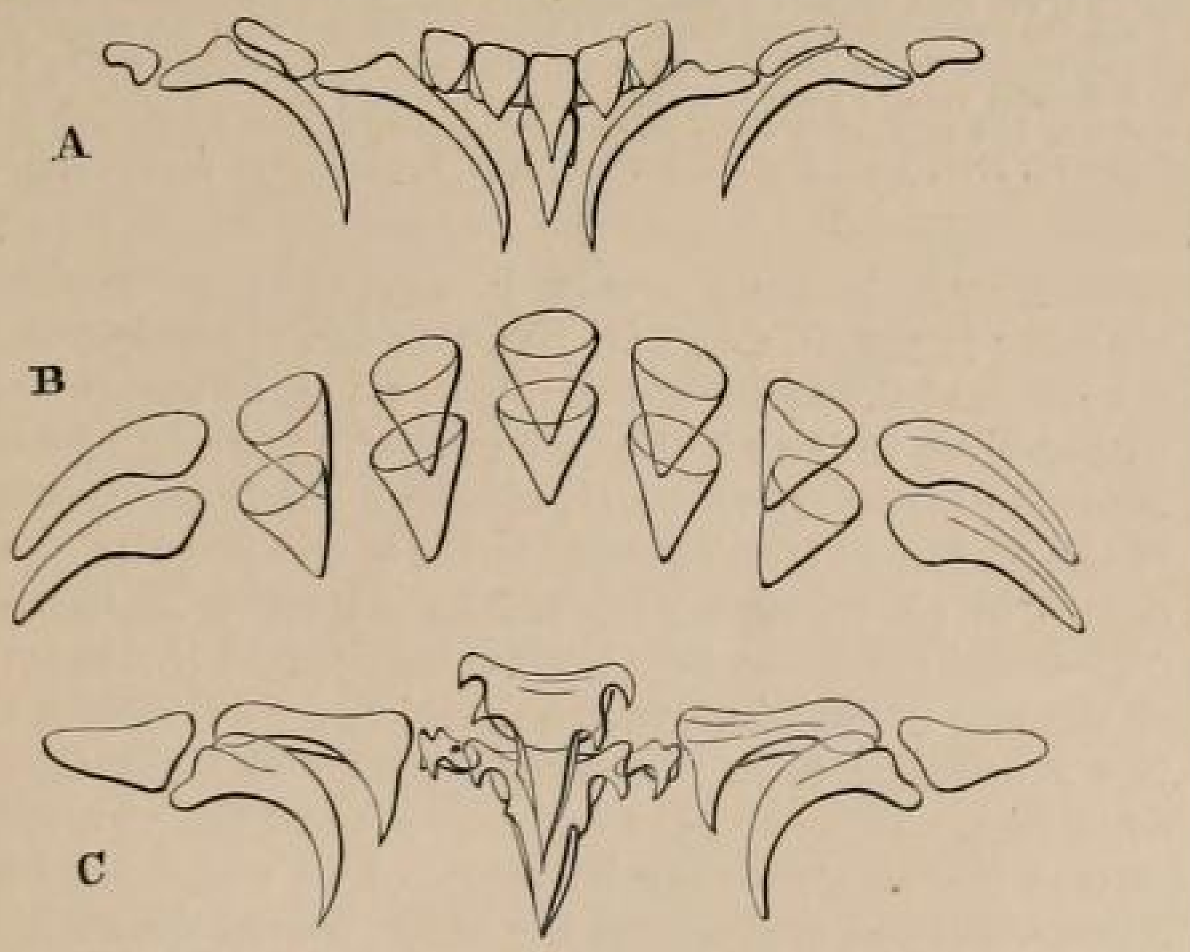


FIG. 107.—Lingual dentition of Siphonopoda. A. A single row of lingual teeth of *Nautilus pompilius* (after Keferstein). B. Two rows of lingual teeth of *Sepia officinalis* (after Troschel). C. Lingual teeth of *Eledone cirrhosa* (after Loven).

Salivary Glands are not developed in Nautilus unless a pair of glandular masses lying on the buccal cavity are to be considered as such. In the Dibranchs, on the contrary, one (Sepia, Loligo) or two pairs of large salivary glands are present, an anterior and a posterior (Octopus, Eledone, Onychoteuthis). Each pair of salivary glands has its paired ducts united to form a single duct, which runs forward from the glands and opens into the buccal cavity near the radula. The anterior pair of glands when present lie in the head near the buccal mass, the posterior pair lie much farther back beneath the liver, at the sides of the œsophagus. It is the posterior pair which alone are present in Sepia and Loligo. The ink-bag is to be considered as an appendage of the rectum. It is not developed in Nautilus, nor in the Pteropoda; in all Dibranchiata (even in the fossil Belemnites) it is present (fig. 106, *a*; fig. 103, *t*), and has been observed to develop as a diverticulum of the rectum, with spirally plaited walls which very early secrete a black pigment. The spiral plaitings of the walls diminish

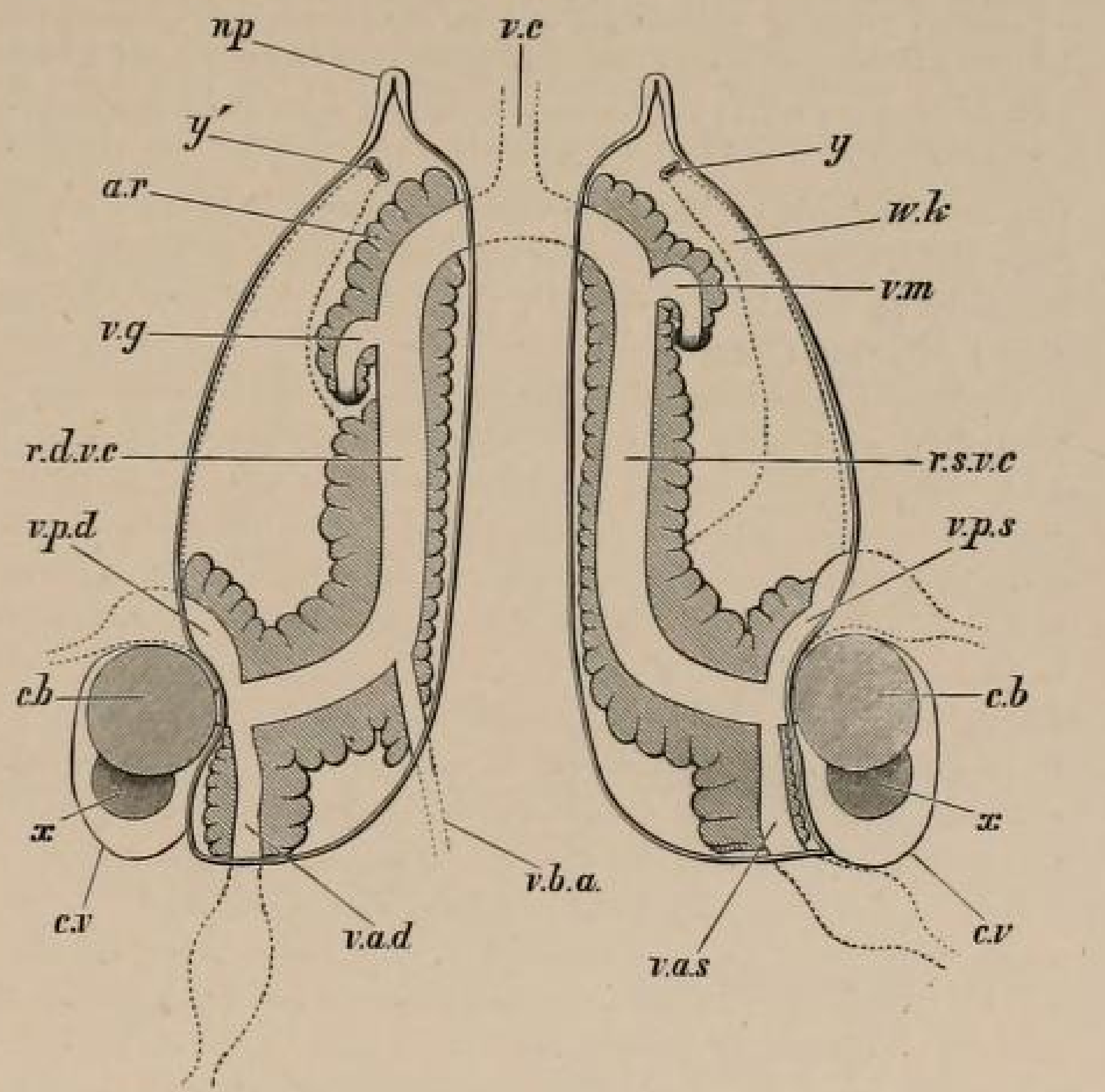


FIG. 108.—Diagram of the nephridial sacs, and the veins which run through them, in *Sepia officinalis* (after Vigelius). The nephridial sacs are supposed to have their upper walls removed. *v.c*, vena cava; *r.d.v.c*, right descending branch of the same; *r.s.v.c*, left descending branch of the same; *v.b.a.*, vein from the ink-bag; *v.m*, mesenteric vein; *v.g*, genital vein; *v.a.d*, right abdominal vein; *v.a.s*, left abdominal vein; *v.p.d*, right pallial vein; *v.p.s*, left pallial vein; *c.b*, branchial heart; *x*, appendage of the same; *c.v*, capsule of the branchial heart; *np*, external aperture of the right nephridial sac; *y*, reno-pericardial orifice placing the left renal sac or nephridium in communication with the viscero-pericardial sac, the course of which below the nephridial sac is indicated by dotted lines; *y′*, the similar orifice of the right side; *a.r*, glandular renal outgrowths; *w.k*, viscero-pericardial sac (dotted outline).

in relative size as the volume of the sac increases. Its outer surface acquires a metallic iridescence similar to that of the integuments of many fishes. The opening of the ink-sac is in the adult sometimes distinct from but near to the anus (Sepia); in other cases it opens into the rectum near the anus. The ink-bag of Dibranch Siphonopoda is possibly to be identified with the adrectal (purpuriparous) gland of some Gastropoda.

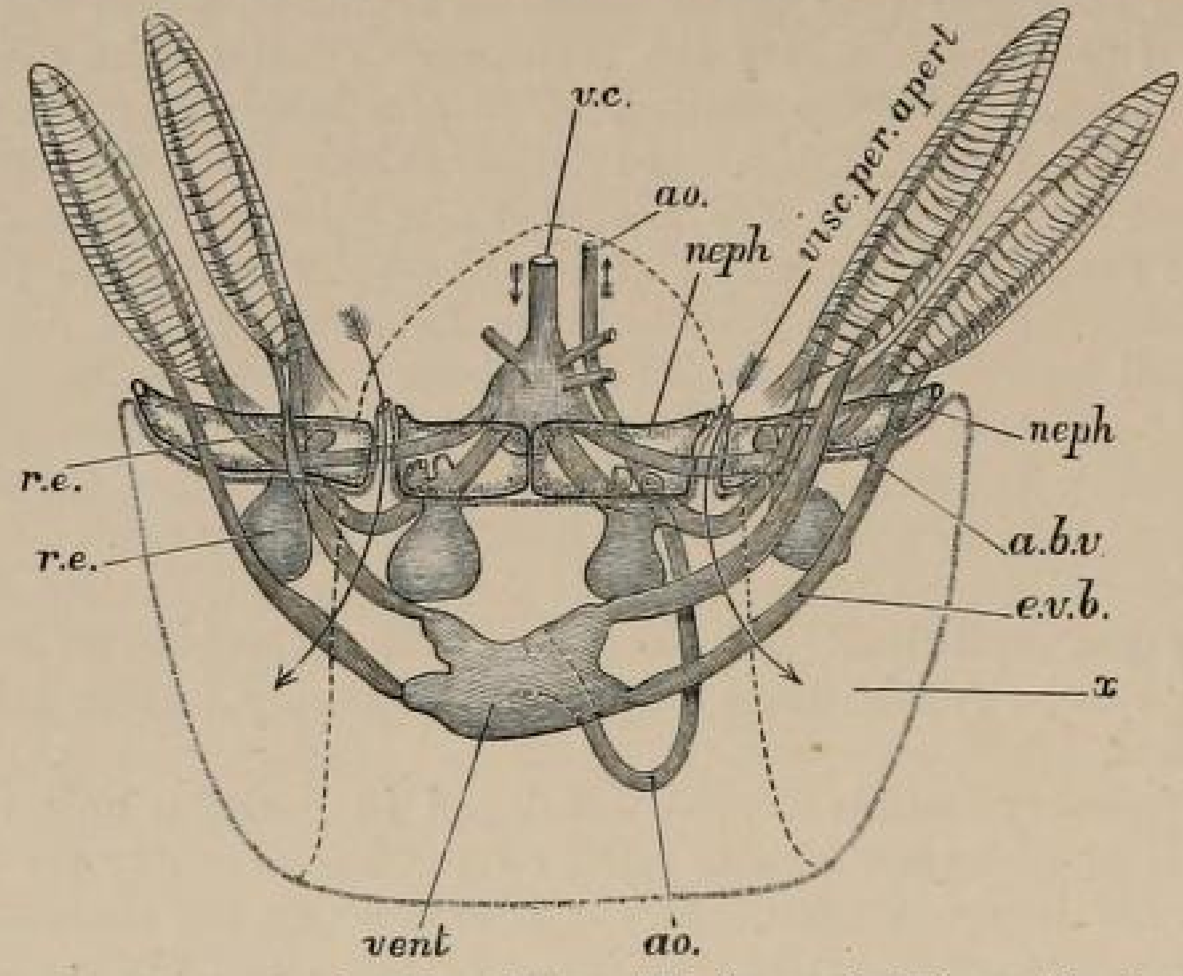


Fig. 109.—Diagram to show the relations of the four nephridial sacs, the viscero-pericardial sac, and the heart and large vessels in Nautilus (drawn by A. G. Bourne). *neph*, *neph*, on the right side point to the two nephridia of that side (the two of the opposite side are not lettered),—each is seen to have an independent aperture; *x* is the viscero-pericardial sac, the dotted line indicating its backward extension; *visc.per.apert* marks an arrow introduced into the right aperture of the viscero-pericardial sac; *r.e.*, *r.e.*, point to the glandular enlarged walls of the advehent branchial vessels,—two small glandular bodies of the kind are seen to project into each nephridial sac, whilst a larger body of the same kind depends from each of the four branchial advehent vessels into the viscero-pericardial sac; *v.c.*, vena cava; *vent*, ventricle of the heart; *ao.*, cephalic aorta (the small abdominal aorta not drawn); *a.b.v*, advehent branchial vessel; *e.v.b.*, efferent branchial vessel.

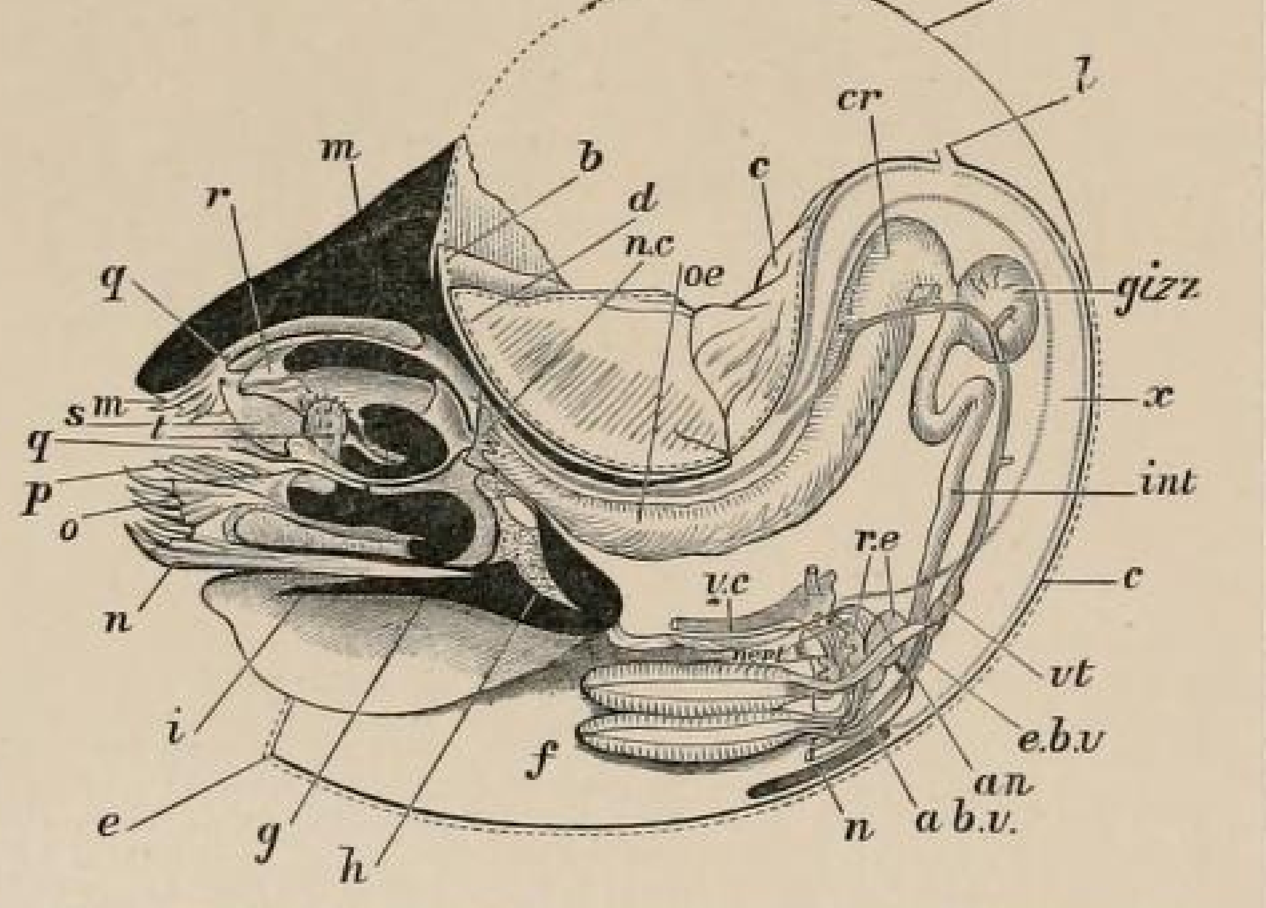


Fig. 110.—Diagram representing a vertical approximately median antero posterior section of *Nautilus pompilius* (from a drawing by A. G. Bourne). The parts which are quite black are the cut muscular surfaces of the foot and buccal mass. *a*, the shell; *b*, the nuchal plate identical with the nuchal cartilage of Sepia (see fig. 90, *b*); *c*, the integument covering the visceral hump; *d*, the mantle flap or skirt in the dorsal region where it rests against the coil of the shell; *e*, the inferior margin of the mantle-skirt resting on the lip of the shell represented by the dotted line; *f*, the pallial chamber with two of the four gills; *g*, the vertically cut median portion of the mid-foot (siphon); *h*, the capito-pedal cartilage (see fig. 116); *i*, the valve of the siphon; *l*, the siphuncular pedicle (cut short); *m*, the hood or dorsal enlargement of the annular lobe of the fore-foot; *n*, tentacles of the annular lobe; *p*, tentacles of the inner inferior lobe; *q*, buccal membrane; *r*, upper jaw or beak; *s*, lower jaw or beak; *t*, lingual ribbon; *x*, the viscero-pericardial sac; *n.c*, nerve-collar; *oe*, œsophagus; *cr*, crop; *gizz*, gizzard; *int*, intestine; *an*, anus; *ni*, nidamental gland; *nept*, aperture of a nephridial sac; *r.e*, renal glandular masses on the walls of the afferent branchial veins (see fig. 109); *a.b.v.*, afferent branchial vessel; *e.b.v*, efferent branchial vessel; *vt*, ventricle of the heart.

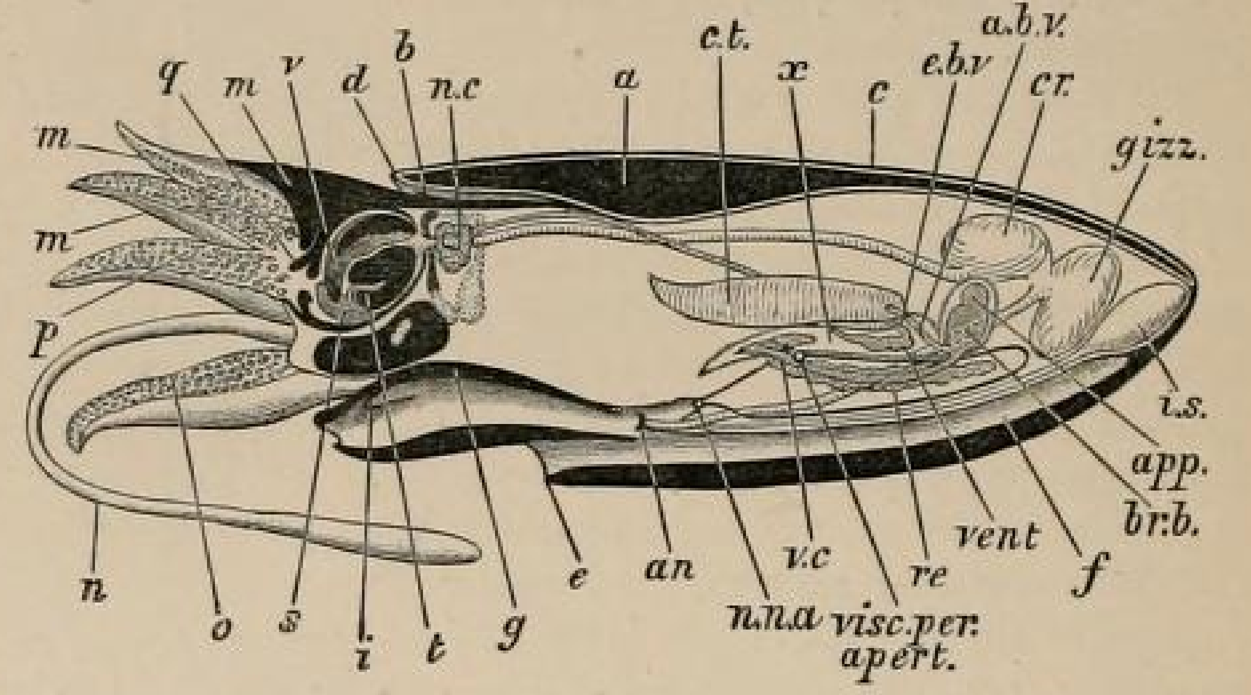


Fig. 111.—Diagram representing a vertical approximately median antero-posterior section of *Sepia officinalis* (from a drawing by A. G. Bourne). The lettering corresponds with that of fig. 110, with which this drawing is intended to be compared. *a*, shell (here enclosed by a growth of the mantle); *b*, the nuchal plate (here a cartilage); *c* (the reference line should be continued through the black area representing the shell to the outline below it), the integument covering the visceral hump; *d*, the reflected portion of the mantle-skirt forming the sac which encloses the shell; *e*, the inferior margin of the mantle-skirt (mouth of the pallial chamber); *f*, the pallial chamber; *g*, the vertically cut median portion of the mid-foot (siphon); *i*, the valve of the siphon; *m*, the two upper lobes of the fore-foot; *n*, the long prehensile arms of the same; *o*, the fifth or lowermost lobe of the fore-foot; *p*, the third lobe of the fore-foot; *q*, the buccal membrane; *v*, the upper beak or jaw; *s*, the lower beak or jaw; *t*, the lingual ribbon; *x*, the viscero-pericardial sac; *n.c*, the nerve-collar; *cr.*, the crop; *gizz.*, the gizzard; *an*, the anus; *c.t.*, the left ctenidium or gill-plume; *vent*, ventricle of the heart; *a.b.v.*, afferent branchial vessel; *e.b.v*, efferent branchial vessel; *re*, renal glandular mass; *n.n.a*, left nephridial aperture; *visc.per.apert.*, viscero-pericardial aperture (see fig. 108); *br.b.*, branchial heart; *app.*, appendage of the same; *i.s.*, ink-bag.

Cœlom, Blood-vascular System, and Excretory Organs.—Nautilus and the other Siphonopoda conform to the general Molluscan characters in regard to these organs. Whilst the general body-cavity or cœlom forms a lacunar blood-system or series of narrow spaces, connected with the trunks of a well-developed vascular system, that part of the original cœlom surrounding the heart and known as the Molluscan pericardium becomes shut off from this general blood-lymph system, and communicates, directly in Nautilus, in the rest through the nephridia, with the exterior. In the Siphonopoda this specialized pericardial cavity is particularly large, and has been recognized as distinct from the blood-carrying spaces, even by anatomists who have not considered the pericardial space of other Mollusca to be thus isolated. The enlarged pericardium, which may even take the form of a pair of sacs, has been variously named, but is best known as the viscero-pericardial sac or chamber. In Nautilus this sac occupies the whole of the postero-dorsal surface and a part of the antero-dorsal (see fig. 110, *x*), investing the genital and other viscera which lie below it, and having the ventricle of the heart suspended in it. Certain membranes forming incomplete septa, and a curious muscular band—the pallio-cardiac band—traverse the sac. The four branchial advehent veins, which in traversing the walls of the four nephridial sacs give off, as it were, glandular diverticula into those sacs, also give off at the same points four much larger glandular masses, which hang freely into the viscero-pericardial chamber (fig. 109, *r.e*). In Nautilus the viscero-pericardial sac opens to the exterior directly by a pair of apertures, one placed close to the right and one close to the left posterior nephridial aperture (fig. 101, *viscper.*). This direct opening of the pericardial sac to the exterior is an exception to what occurs in all other Mollusca. In all other Molluscs the pericardial sac opens into the nephridia, and through them or the one nephridium to the exterior. In Nautilus there is no opening from the viscero-pericardial sac into the nephridia. Therefore the external pore of the viscero-pericardial sac may possibly be regarded as a shifting of the reno-pericardial orifice from the actual wall of the nephridial sac to a position alongside of its orifice. Parallel cases of such shifting are seen in the varying position of the orifice of the ink-bag in Dibranchiata, and in the orifice of the genital ducts of Mollusca, which in some few cases (*e.g.*, Spondylus) open into the nephridia, whilst in other cases they open close by the side of the nephridia on the surface of the body. The viscero-pericardial sac of the

Dibranchs is very large also, and extends into the dorsal region. It varies in shape—that is to say, in the extensions of its area right and left between the various viscera—in different genera, but in the Decapods is largest. In an extension of this chamber is placed the ovary of Sepia, whilst the ventricle of the heart and the branchial hearts and their appendages also lie in it. It is probable that water is drawn into this chamber through the nephridia, since sand and other foreign matters are found in it. In all it opens into the pair of nephridial sacs by an orifice on the wall of each, not far from the external orifice (fig. 108, *y*, *y'*). There does not seem any room for doubting that each orifice corresponds to the reno-pericardial orifice which we have seen in the Gastropoda, and shall find again in the Lamellibranchia. The single tube-like nephridium and the pericardium of the Pteropoda also communicate by an aperture.

The circulatory organs, blood-vessels, and blood of Nautilus do not differ greatly from those of Gastropoda. The ventricle of the heart is a four-cornered body, receiving a dilated branchial efferent vessel (auricle) at each corner (fig. 109). It gives off a cephalic aorta anteriorly, and a smaller abdominal aorta posteriorly. The diagram, fig. 105, serves to show how this simple form of heart is related to the dorsal vessel of a worm or of an Arthropod, and how by a simple flexure of the ventricle (D) and a subsequent suppression of one auricle, following on the suppression of one branchia, one may obtain the form of heart characteristic of the Anisopleurous Gastropoda (excepting the Zygobranchia). The flexed condition of the heart is seen in Octopus, and is to some extent approached by Nautilus, the median vessels not presenting that perfect parallelism which is shown in the figure (B). The most remarkable feature presented by the heart of Nautilus is the possession of four instead of two auricles, a feature which is simply related to the metamerism of the branchiæ. By the left side of the heart of Nautilus, attached to it by a membrane, and hanging loosely in the viscero-pericardial chamber, is the pyriform sac of Owen. This has recently been shown to be the rudimentary left oviduct or sperm-duct, as the case may be (Lankester and Bourne, **37**), the functional right ovi-sac and its duct being attached by a membrane to the opposite side of the heart.

The cephalic and abdominal aortæ of Nautilus appear, after running to the anterior and posterior extremes of the animal respectively, to open into sinus-like spaces surrounding the viscera, muscular masses, &c. These spaces are not large, but confined and shallow. Capillaries are stated to occur in the integument. In the Dibranchs the arterial system is very much more complete; it appears in some cases to end in irregular lacunæ or sinuses, in other cases in true capillaries which lead on into veins. An investigation of these capillaries in the light of modern histological knowledge is much needed. From the sinuses and capillaries the veins take origin, collecting into a large median trunk (the vena cava), which in the Dibranchs as well as in Nautilus has a ventral (postero-ventral) position, and runs parallel to the long axis of the animal. In Nautilus this vena cava gives off at the level of the gills four branchial advehent veins (fig. 109, *v.c.*), which pass into the four gills without dilating. In the Dibranchs at a similar position the vena cava gives off a right and a left branchial advehent vein (fig. 108, *r.s.v.c*, *r.d.v.c*), each of which, traversing the wall of the corresponding nephridial sac and receiving additional factors (fig. 108, *v.g*, *v.p.d*, *v.a.d*, *v.b.a*), dilates at the base of the corresponding branchial plume, forming there a pulsating sac—the branchial heart (fig. 104, *x*; and fig 108, *c.b*). Attached to each branchial heart is a curious glandular body, which may possibly be related to the larger masses (*r.e* in fig. 109) which depend into the viscero-pericardial cavity from the branchial advehent veins of Nautilus. From the dilated branchial heart the branchial advehent vessel proceeds, running up the ad-pallial face of the gill-plume (*vi*, *vc'*, fig. 104). From each gill-plume the blood passes by the branchial efferent vessels (*v'*, fig. 104) to the heart, the two auricles being formed by the dilatation of these vessels (*v*, *v* in fig. 104).

The blood of Siphonopoda contains the usual amœboid corpuscles, and a diffused colouring matter—the hæmocyanin of Fredericque—which has been found also in the blood of Helix, and in that of the Arthropods Homarus and Limulus. It is colourless in the oxidized, blue in the deoxidized state, and contains copper as a chemical constituent.

The nephridial sacs and renal glandular tissue are closely connected with the branchial advehent vessels in Nautilus and in the other Siphonopoda. The arrangement is such as to render the typical relations and form of a nephridium difficult to trace. In accordance with the metamerism of Nautilus already noticed, there are two pairs of nephridia. Each nephridium assumes the form of a sac opening by a pore to the exterior. As is usual in nephridia, a glandular and a non-glandular portion are distinguished in each sac; these portions, however, are not successive parts of a tube, as happens in other cases, but they are localized areæ of the wall of the sac. The glandular renal tissue is, in fact, confined to a tract extending along that part of the sac's wall which immediately invests the great branchial advehent vein. The vein in this region gives off directly from its wall a complete herbage of little venules, which branch and anastomose with one another, and are clothed by the glandular epithelium of the nephridial sac. The secretion is accumulated in the sac and passed by its aperture to the exterior. Probably the nitrogenous excretory product is very rapidly discharged; in Nautilus a pink-coloured powder is found accumulated in the nephridial sacs, consisting of calcium phosphate. The presence of this phosphatic calculus by no means proves that such was the sole excretion of the renal glandular tissue. In Nautilus a glandular growth like that rising from the wall of the branchial vessel into its corresponding nephridial sac, but larger in size, depends from each branchial advehent vessel into the viscero-pericardial sac,—probably identical with the "appendage" of the branchial hearts of Dibranchs.

The chief difference, other than that of number between the nephridia of the Dibranchs and those of Nautilus, is the absence of the accessory growths depending into the viscero-pericardial space just mentioned, and, of more importance, the presence in the former of a pore leading from the nephridial sac into the viscero-pericardial sac (*y*, *y'* in fig. 108). The external orifices of the nephridia are also more prominent in Dibranchs than in Nautilus, being raised on papillæ (*np* in fig. 108; *r* in fig. 103). In Sepia, according to Vigelius (**38**), the two nephridia give off each a diverticulum dorsalwards, which unites with its fellows and forms a great median renal chamber, lying between the ventral portions of the nephridia and the viscero-pericardial chamber. In Loligo the fusion

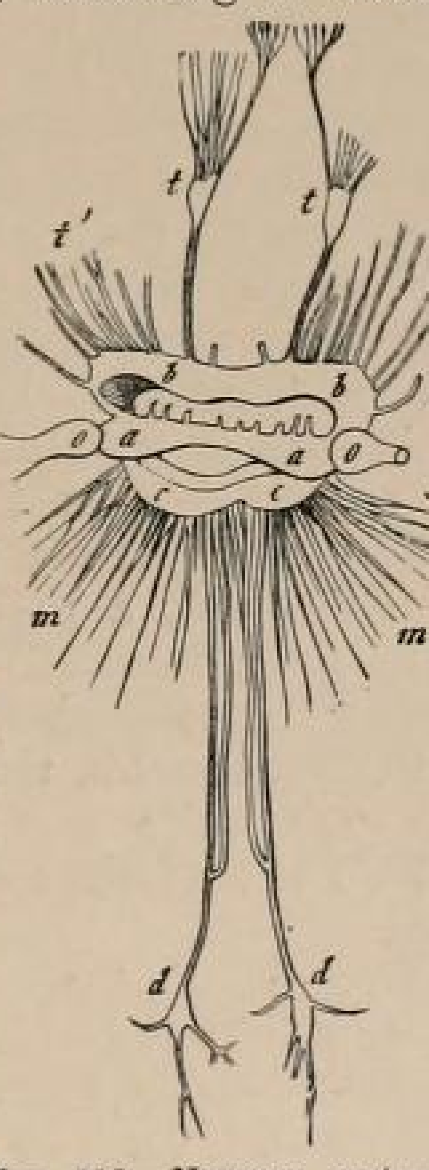


FIG. 112.—Nervous system of *Nautilus pompilius* (from Gegenbaur, after Owen). *t*, *t*, ganglion-like enlargements on nerves passing from the pedal ganglion to the inner series of tentacles; *t'*, nerves to the tentacles of the outer or annular lobe; *b*, pedal ganglion-pair; *a*, cerebral ganglion-pair); *c*, pleuro-visceral ganglionic band (fused pleural and visceral ganglion-pairs); *d*, genital ganglion placed on the course of the large visceral nerve, just before it gives off its branchial and its osphradial branches; *m*, nerves from the pleural ganglion to the mantle-skirt.

of the two nephridia to form one sac is still more obvious, since the ventral portions are united. In Octopus the nephridia are quite separate.

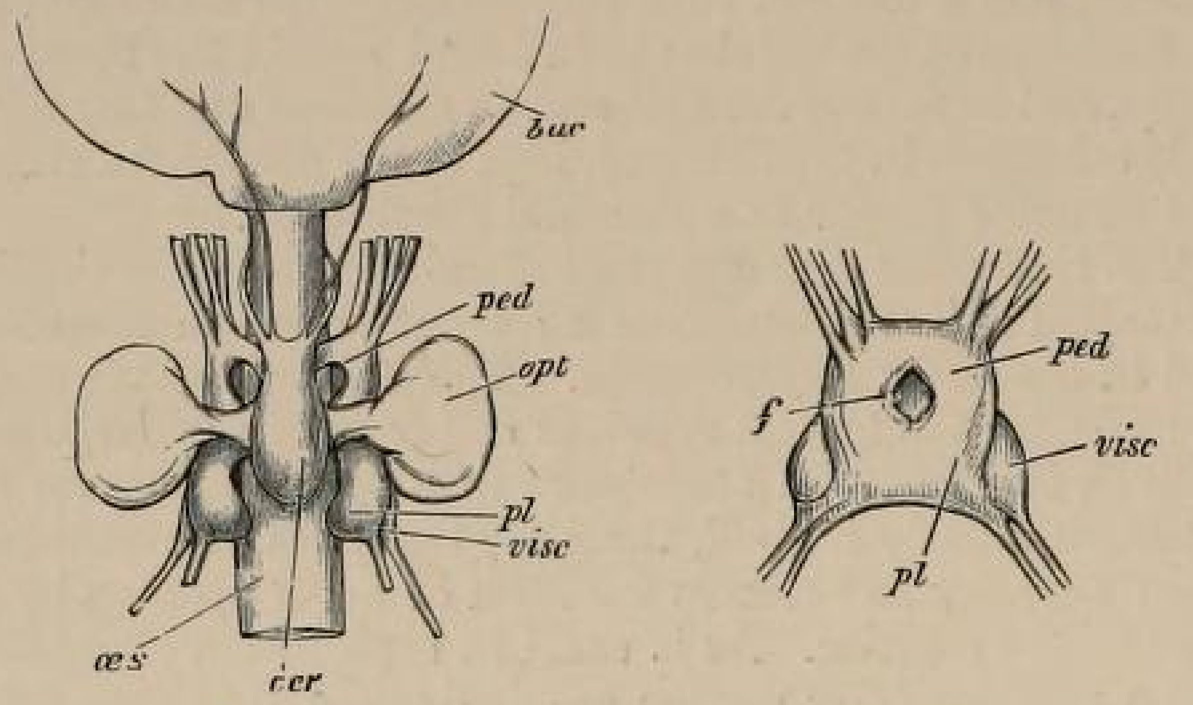


Fig. 113. Fig. 114.

FIGS. 113, 114.—Nerve-centres of Octopus. Figure 113 gives a view from the dorsal aspect, figure 114 one from the ventral aspect. *buc*, the buccal mass; *ped*, pedal ganglion; *opt*, optic ganglion; *cer*, cerebral ganglion; *pl*, pleural ganglion; *visc*, visceral ganglion; *œs*, œsophagus; *f*, foramen in the nerve-mass formed by pedal, pleural, and visceral ganglion-pairs, traversed by a blood-vessel.

Tegumental pores have not been described in Nautilus, but exist in Dibranchiata, and have been (probably erroneously, but further investigation is needed) supposed to introduce water into the vascular system. A pair of such pores leading into sub-tegumental spaces of considerable area, the nature of which is imperfectly known, exist on the back of the head in Philonexis, Tremoctopus, and Argonauta. At the base of the arms and mouth four such pores are found in Histioteuthis and Ommastrephes, six in Sepia, Loligo, Onychoteuthis. Lastly, a pair of such pores are found in the Decapoda at the base of the long arms, leading into an extensive sub-tegumental pouch on each side of the head into which the long arms can be, and usually are, withdrawn. In Sepia, Sepiola, and Rossia the whole arm is coiled up in these sacs; in Loligo only a part of it is so; in Histioteuthis, Ommastrephes, and Onychoteuthis, the sacs are quite small and do not admit the arms.

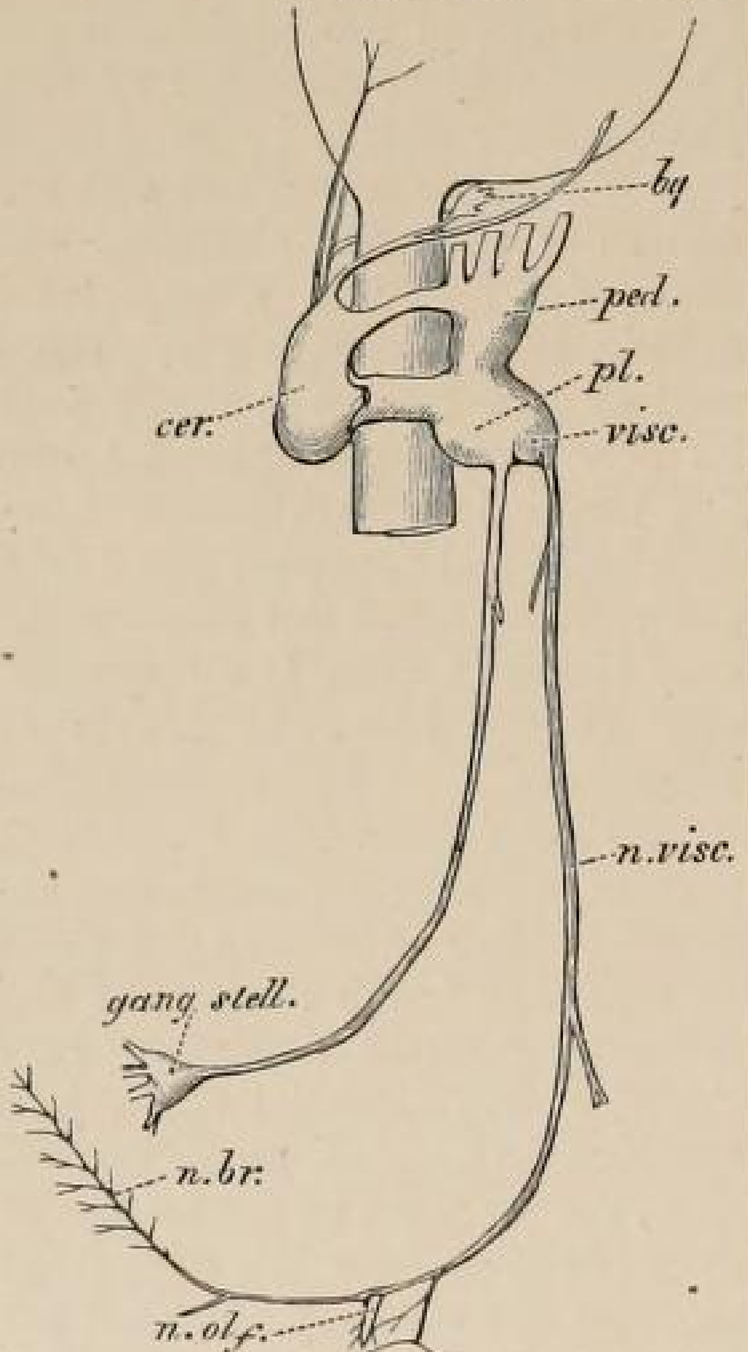


FIG. 115.—Lateral view of the nervous centres and nerves of the right side of *Octopus vulgaris* (from a drawing by A. G. Bourne). *bg*, buccal ganglion; *cer.*, cerebral ganglion; *ped.*, pedal ganglion; *pl.*, pleural, and *visc.*, visceral region of the pleuro-visceral ganglion; *gang. stell.*, the right stellate ganglion of the mantle connected by a nerve to the pleural portion; *n.visc.*, the right visceral nerve; *n.olf.*, its (probably) olfactory branches; *n.br.*, its branchial branches.

Nervous System.—Nautilus, like the other Cephalopoda (*e.g.*, Pneumodermon, fig. 87; Octopus, fig. 113), exhibits a great concentration of the typical Molluscan ganglia, as shown in fig. 112. The ganglia take on a band-like form, and are but little differentiated from their commissures and connectives,—an archaic condition reminding us of Chiton. The special optic outgrowth of the cerebral ganglion, the optic ganglion (fig. 112, *o*), is characteristic of the big-eyed Siphonopoda. The cerebral ganglion-pair (*a*) lying above the œsophagus is connected with two sub-œsophageal ganglion-pairs of band-like form. The anterior of these is the pedal *b*, *b*, and supplies the fore-foot with nerves *t′*, *t*, as also the mid-foot (siphon). The hinder band is the visceral and pleural pair fused (compare fig. 112 with fig. 87, and especially with the typical Euthyneurous nervous system of Limnæus, fig. 22); from its pleural portion nerves pass to the mantle, from its visceral portion nerves to the branchiæ and genital ganglion (*d* in fig. 112), and in immediate connexion with the latter is a nerve to the osphradium or olfactory papilla. No buccal ganglia have been observed in Nautilus, nor has an enteric nervous system been described in this animal, though both attain a special development in the Dibranchiata. The figures (114 and 115) representing the nerve-centres of Octopus serve to exhibit the disposition of these parts in the Dibranchiata. The ganglia are more distinctly swollen than in Nautilus. In Octopus an infra-buccal ganglion-pair are present corresponding to the buccal ganglion-pair of Gastropoda. In Decapoda a supra-buccal ganglion-pair connected with these are also developed. Instead of the numerous radiating pallial nerves of Nautilus, we have in the Dibranchiata on each side (right and left) a large pleural erve passing from the pleural portion of the pleuro-visceral ganglion to the mantle, where it enlarges to form the stellate ganglion. From each stellate ganglion nerves radiate to supply the powerful muscles of the mantle-skirt. The nerves from the visceral portion of the pleuro-visceral ganglion have the same course as in Nautilus, but no osphradial papilla is present. An enteric nervous system is richly developed in the Dibranchiata, connected with the somatic nervous centres through the buccal ganglia, as in the Arthropoda through the stomato-gastric ganglia, and anastomosing with deep branches of the visceral nerves of the viscero-pleural ganglion-pair. It has been especially described by Hancock (**39**) in Ommastrephes. Upon the stomach it forms a single large and readily-detected gastric ganglion. It is questionable as to how far this and the "caval ganglion" formed in some Decapoda by branches of the visceral nerves which accompany the vena cava are to be considered as the equivalents of the "abdominal ganglion," which in a typical Gastropod nervous system lies in the middle of the visceral nerve-loop or commissure, having the right and left visceral ganglia on either side of it, separated by a greater or less length of visceral nerve-cord (see figs. 20, 21, 22). There can be little doubt that the enteric nervous system is much more developed in the Dibranchiata than in other Mollusca, and that it effects a fusion with the typical "visceral" cords more extensive than obtains even in Gastropoda, where such a fusion no doubt must also be admitted.

Special Sense-Organs.—Nautilus possesses a pair of osphradial papillæ (fig. 101, *olf*) corresponding in position and innervation to Spengel's organ placed at the base of the ctenidia (branchiæ) in all classes of Mollusca. This organ has not been detected in other Siphonopoda. In Pteropoda it is well developed as a single ciliated pit, although the ctenidia are in that group aborted (fig. 87, *Osp.*). Nautilus possesses other olfactory organs in the region of the head. Just below the eye is a small triangular process (not seen in our figures), having the structure of a shortened and highly-modified tentacle and sheath. By Valenciennes, who is followed by Keferstein, this is regarded as an olfactory organ. The large nerve which runs to this organ originates from the point of juncture of the pedal with the optic ganglion. The lamelliform organ upon the inner inferior tentacular lobe of Nautilus is possibly also olfactory in function. In Dibranchs behind the eye is a pit or open canal supplied by a nerve corresponding in origin to the olfactory nerve of Nautilus above mentioned.

Possibly the sense of taste resides in certain processes within the mouth of Nautilus and other Siphonopoda.

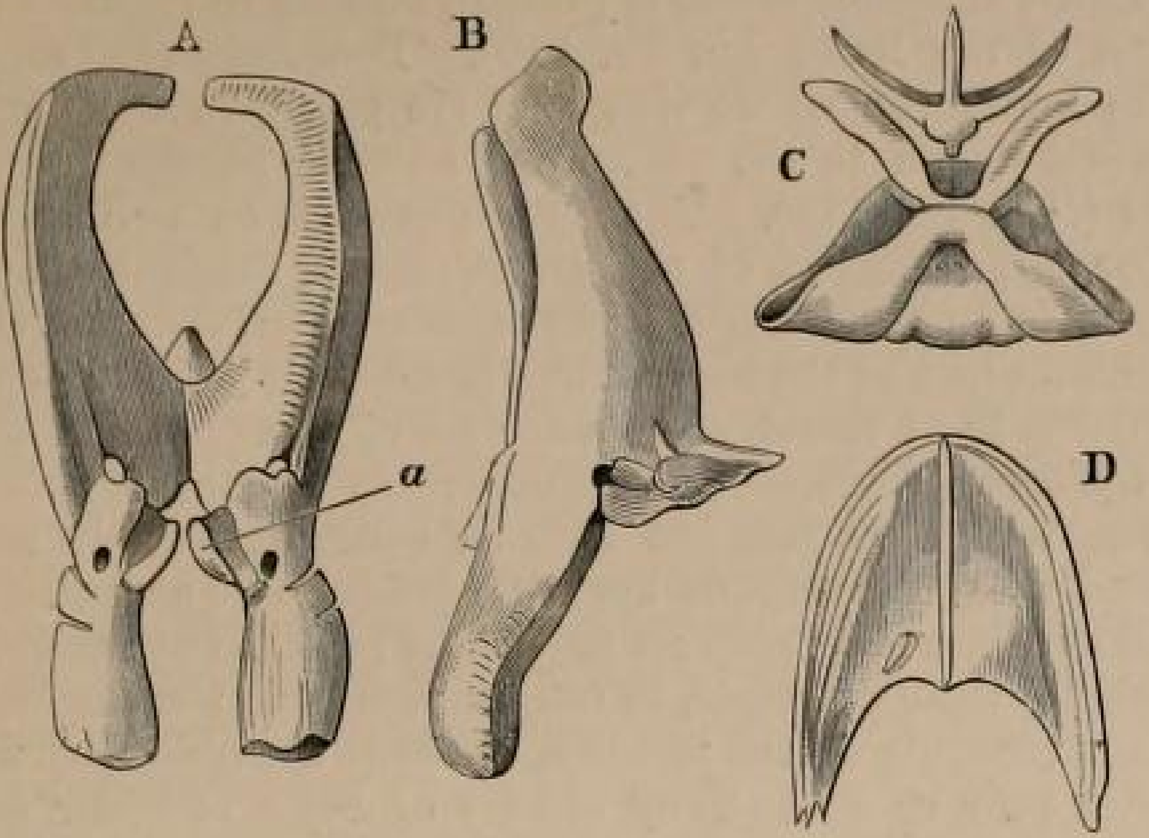


Fig. 116.—Cartilaginous skeleton of Siphonopoda (after Keferstein). A. Capito-pedal cartilage of *Nautilus pompilius*; *a* points to the ridge which supports the pedal portion of the nerve-centre. B. Lateral view of the same,—the large anterior processes are sunk in the muscular substance of the siphon. C. Cephalic cartilages of *Sepia officinalis*. D. Nuchal cartilage of *Sepia officinalis*.

The otocysts of Nautilus were discovered by Macdonald (**40**). Each lies at the side of the head, ventral of the eye, resting on the capito-pedal cartilage, and supported by the large auditory nerve which arises from the pedal ganglion. It has the form of a small sac, 1 to 2 mm. in diameter, and contains whetstone - shaped crystals, such as are known to form the otoliths of other Mollusca. The otocysts of Dibranchiata are larger and deeply sunk in the cephalic cartilage. It has been shown by Lankester that they develop as open pits (fig. 121, (5), (6), *o*), which gradually close up, the communication with the exterior becoming narrowed into a fine canal, which is reflected over one end of the sac, and finally has its external opening obliterated. A single otolith only is found in all Dibranchiata.

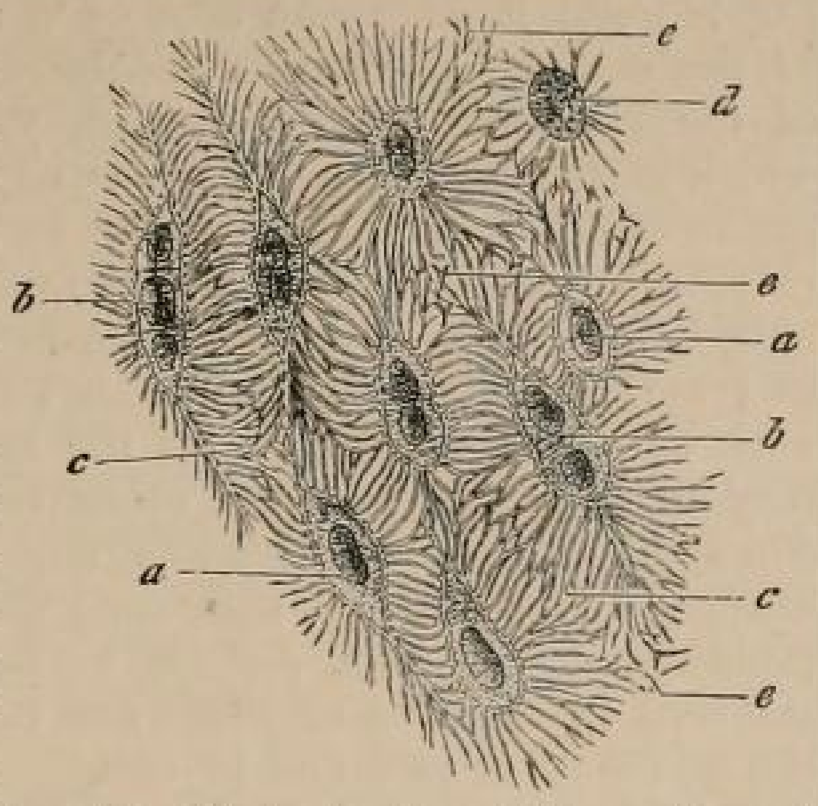


Fig. 117.—Minute structure of the cartilage of Loligo (from Gegenbaur, after Furbringer). *a*, simple, *b*, dividing, cells; *c*, canaliculi; *d*, an empty cartilage capsule with its pores; *e*, canaliculi in section.

The eye of Nautilus is among the most interesting structures of that remarkable animal. No other animal which has the same bulk and general elaboration of organization has so simple an eye as that of Nautilus. When looked at from the surface no metallic lustre, no transparent coverings, are presented by it. It is simply a slightly projecting hemispherical box like a kettle-drum, half an inch in diameter, its surface looking like that of the surrounding integument, whilst in the middle of the drum-membrane is a minute hole (fig. 91, *u*). Owen very naturally thought that some membrane had covered this hole in life, and had been ruptured in the specimen studied by him. It, however, appears from the researches of Hensen (**41**) that the hole is a normal aperture leading into the globe of the eye, which is accordingly filled by sea-water during life. There is no dioptric apparatus in Nautilus, and in place of refracting lens and cornea we have actually here an arrangement for forming an image on the principle of "the pin-hole camera." There is no other eye known in the whole animal kingdom which is so constructed. The wall of the eye-globe is tough, and the cavity is lined solely by the naked retina, which is bathed by sea-water on one surface and receives the fibres of the optic nerve on the other (see fig. 118, A). As in other Siphonopods (*e.g.*, fig. 120, *Ri*, *Re*, *p*), the retina consists of two layers of cells separated by a layer of dark pigment. The most interesting consideration connected with this eye of Nautilus is found when the further facts are noted—(1) that the elaborate lens-bearing eyes of Dibranchiata pass through a stage of development in which they have the same structure as the eye of Nautilus —namely, are open sacs (fig. 119); and (2), that amongst other Mollusca examples of cephalic eyes can be found which in the adult condition are, like the eye of Nautilus and the developing eye of Dibranchs, simple pits of the integument, the cells of which are surrounded by pigment and connected with the filaments of an optic nerve. Such is the structure of the eye of the Limpet (Patella); and in such a simple eye we obtain the clearest demonstration of the fact that the retina of the Molluscan cephalic eye, like that of the Arthropod cephalic eye and unlike that of the Vertebrate myelonic eye, is essentially a modified area of the general epiderm, and that the sensitiveness of its cells to the action of light and their relation to nerve-filaments is only a specialization and intensifying of a property common to the whole epiderm of the surface of the body. What, however, strikes us as especially remarkable is that the simple form of a pit, which in Patella serves to accumulate a secretion which acts as a refractive body, should in Nautilus be glorified and raised to the dignity of an efficient optical apparatus. Natural selection has had an altogether exceptional opportunity in the ancestors of Nautilus. In all other Mollusca, starting as we may suppose from the follicular or pit-like condition, the eye has proceeded to acquire the form of a *closed* sac, the cavity of the closed vesicle being then filled partially or completely by a refractive body (lens) secreted by its walls (fig. 118, B). This is the condition attained in most Gastropoda. It presents a striking contrast to the simple Arthropod eye, where, in consequence of the existence of a dense exterior cuticle, the eye does not form a vesicle, and the lens is always part of that cuticle.

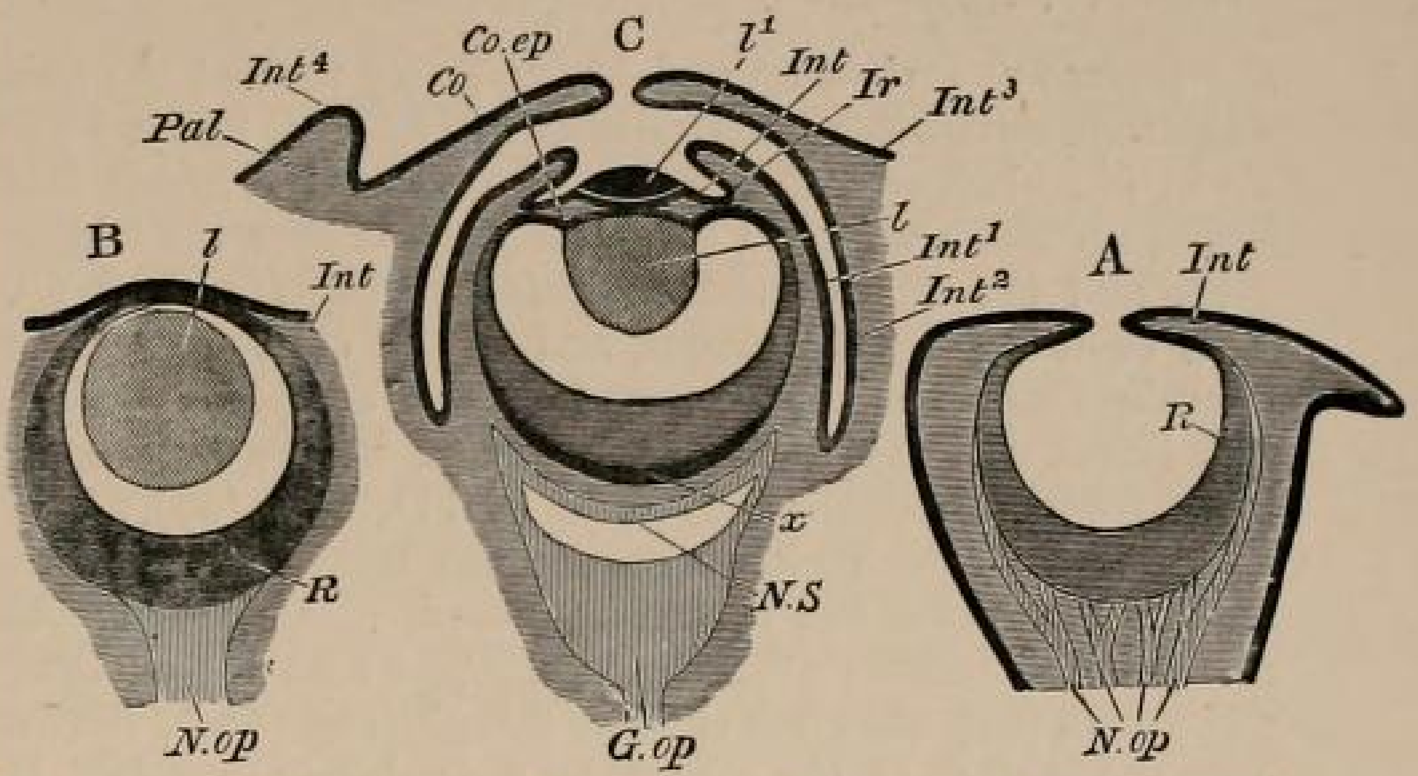


Fig. 118.—Diagrams of sections of the eyes of Mollusca. A. Nautilus (and Patella). B. Gastropod (Limax or Helix). C. Dibranchiate Siphonopod (Oigopsid). *Pal*, eyelid (outermost fold); *Co*, cornea (second fold); *Ir*, iris (third fold); $Int^1, {}^2, {}^3, {}^4$, different parts of the integument; *l*, deep portion of the lens; l^1, outer portion of the lens; *Co.ep*, ciliary body; *R*, retina; *N.op*, optic nerve; *G.op*, optic ganglion; *x*, inner layer of the retina; *N.S*, nervous stratum of the retina. (From Balfour, after Grenacher.)

In the Dibranchiate division of the Siphonopoda the greatest elaboration of the dioptric apparatus of the eye is attained, so that we have in one sub-class the extremes of the two lines of development of the Molluscan eye, those two lines being the punctigerous and the lentigerous. The structure of the Dibranchiate's eye is shown in section in fig. 118, C, and in fig. 120, and its development in fig. 119 and fig. 123. The open sac which forms the retina of the young Dibranchiate closes up, and constitutes the posterior chamber of the eye, or primitive optic vesicle (fig. 123, A, *poc*). The lens forms as a structureless growth, projecting inwards from the front wall of this vesicle (fig. 123, B, *l*). The integument around the primitive optic vesicle which has sunk below the surface now rises up and forms firstly nearest the axis of the eye the iridian folds (*if* in B, fig. 123 ; *ik* in fig. 120 ; *Ir* in fig. 118), and then secondly an outer circular fold grows up like a wall and completely closes over the iridian folds and the axis of the primitive vesicle (fig. 120, C). This covering is transparent, and is the cornea. In the oceanic Decapoda the cornea does not completely close, but leaves a central aperture traversed by the optic axis. These forms are termed Oigopsidæ by d'Orbigny (**42**), whilst the Decapoda with closed cornea are termed Myopsidæ. In the Octopoda the cornea is closed, and there is yet another fold thrown over the eye. The skin surrounding the cornea presents a free circular margin, and can be drawn over the surface of the cornea by a sphincter muscle. It thus acts as an adjustable diaphragm, exactly similar in movement to the iris of Vertebrates. Sepia and allied Decapods have a horizontal lower eyelid, that is to say, only one-half of the sphincter-like fold of integument is movable. The exact history of the later growth of the lens in the Dibranchs' eye is not clear. As seen in fig. 120, it appears, after attaining a certain size, to push through the front wall of the primitive optic vesicle at the point corresponding to its centre of closure, and to project a little into the anterior chamber formed by the cornea. The wall of the primitive optic vesicle adjacent to the embedded lens (L) now becomes modified, forming a so-called "ciliary body," in which muscular tissue is present, serving to regulate the focus of the lens (*ci* in fig. 120). Bobretzky (**43**) differs from Lankester, whose view is above given, in assigning a distinct origin to the protruding anterior segment of the lens (l^1 in fig. 118). The optic ganglion, as well as the other large ganglia of the Dibranchiata, originate in the mesoblast of the embryo. The connexion between the cells of the retina and the nerve-fibres proceeding from the optic ganglion must therefore be a secondary one.

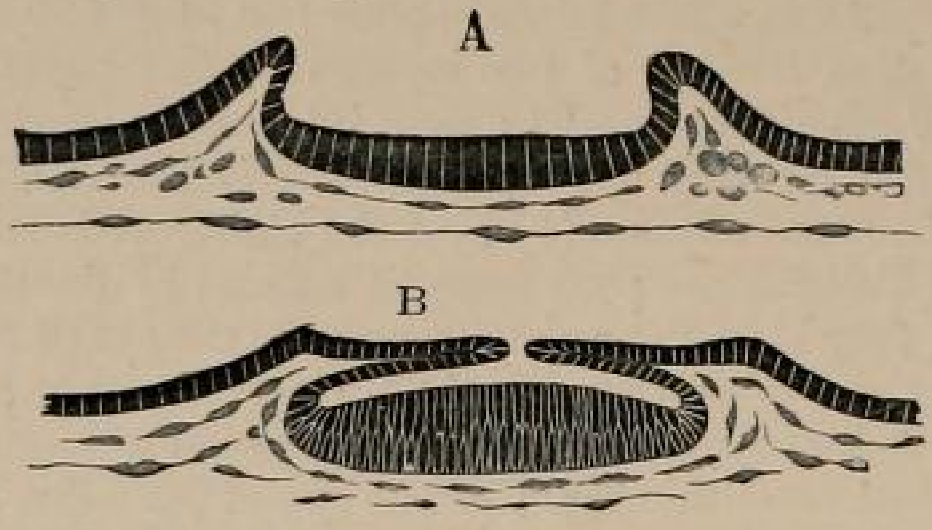


FIG. 119.—Diagrams of sections showing the early stage of development of the eye of Loligo when it is, like the permanent eye of Nautilus and of Patella, an open sac. A. First appearance of the eye as a ring-like upgrowth. B. Ingrowth of the ring-like wall so as to form a sac, the primitive optic vesicle of Loligo. (From Lankester.)

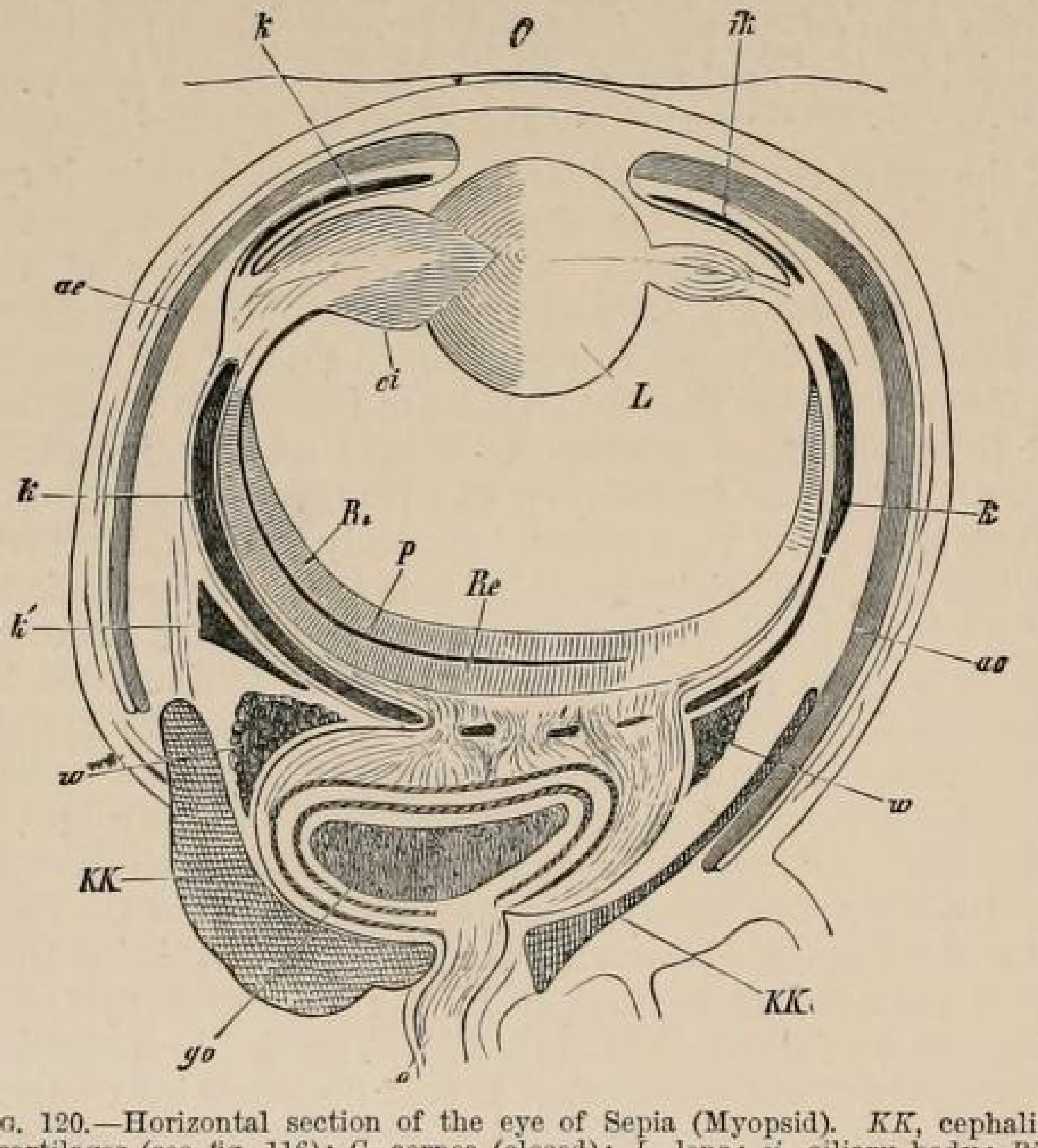


FIG. 120.—Horizontal section of the eye of Sepia (Myopsid). *KK*, cephalic cartilages (see fig. 116); *C*, cornea (closed); *L*, lens; *ci*, ciliary body; *Ri*, internal layer of the retina; *Re*, external layer of the retina; *p*, pigment between these; *o*, optic nerve; *go*, optic ganglion; *k* and *k'*, capsular cartilage; *ik*, cartilage of the iris; *w*, white body; *ae*, argentine integument. (From Gegenbaur, after Hensen.)

Chromatophores.—In Nautilus these remarkable structures, which we mention here as being intimately associated with the nervous system, appear to be absent. In Dibranchiata they play an important part in the economy, enabling their possessor, in conjunction with the discharge of the contents of the ink-bag, to elude the observation of either prey or foe. They consist of large vesicular cells (true nucleated cells converted into vesicles), arranged in a layer immediately below the epidermis. Each chromatophore-cell has from six to ten muscular bands attached to its walls, radiating from it star-wise. The contraction of these fibres causes the chromatophore-cell to widen out; it returns to its spherical resting state by its own elasticity. In the spherical resting state such a cell may measure ·01 mm., whilst when fully stretched by its radiating muscles it covers an area of ·5 mm. The substance of the chromatophore-cells is intensely coloured with one of the following colours—scarlet, yellow, blue, brown—which are usually of the greatest purity and brilliance. The action of the chromatophores may be watched most readily in young Loligo, either under the microscope or with the naked eye. The chromatophores are suddenly expanded, and more slowly retracted with rapidly-recurring alternation. All the blue, or all the red, or all the yellow may be expanded and the other colours left quiescent. Thus the animal can assume any particular hue, and change its appearance in a dazzling way with extraordinary rapidity. There is a definite adaptation of the colour assumed in the case of Sepia and others to the colour of the surrounding rock and bottom.

Gonads and Genital Ducts.—In Nautilus it has recently been shown by Lankester and Bourne (**37**) that the genital ducts of both sexes are paired right and left, the left duct being rudimentary and forming the "pyriform appendage," described by Owen as adhering by membranous attachment to the ventricle of the heart, and shown by Keferstein to communicate by a pore with the exterior. Thus the Cephalopoda agree with our archi-Mollusc in having bilaterally symmetrical genital ducts in the case of the most archaic member of the class. The ovary (female gonad) or the testis (male gonad) lies in Nautilus as in the Dibranchs in a distinct cavity walled off from the other viscera, near the centro-dorsal region. This chamber is formed by the cœlomic or peritoneal wall; the space enclosed is originally part of the cœlom, and in Sepia and Loligo is, in the adult, part of the viscero-pericardial chamber. In Octopus it is this genital chamber which communicates by a right and a left canal with the nephridium, and is the only representative of pericardium. The ovary or testis is itself a growth from the inner wall of this chamber, which it only partly fills. In Nautilus the right genital duct, which is functional, is a simple continuation to the pore on the postero-dorsal surface of the membranous walls of the capsule in which lies the ovary or the testis, as the case may be. The gonad itself appears to represent a single median or bilateral organ.

The true morphological nature of the genital ducts of the Cephalopoda and of other Mollusca is a subject which invites speculation and inquiry. In all the cases in which such ducts continuous with the tunic of the gonad itself occur—viz., in Nematoid worms, in Arthropoda, and in Teleostean fishes, besides Mollusca—there is an absence of definite knowledge as to the mode of development of the duct. It seems, however, from such facts as have been ascertained that the gonad lies at first freely in the cœlom, and that the duct develops in connexion with the genital pore, and attaches itself to the embryonic gonad, or to the capsule which grows around it. The question then arises as to the nature of the pore. In other groups of animals we find that the pore, and funnel or tube connected with it by which the genital products are conveyed to the exterior, is a modified nephridium (usually a pair, one right and one left). Is it possible that this is also the case where the duct very early becomes united to the gonad, and even gives rise to the appearance of a tubular ovary or testis? Probably this is the case in Teleostean fishes (see Huxley's observations on the oviducts of the smelt, **44**); but it seems to be a tenable position that in other cases, including the Mollusca, the genital pore is a simple opening in the body-wall leading into the body-cavity or cœlom, such as we find on the dorsal surface of the earth-worm, which has become specialized for the extrusion of the genital products. Possibly, as in Nemertine and Chætopod worms, the condition preceding the development of these definite genital pores was one in which a temporary rupture of the body-wall occurred at the breeding season, and this temporary aperture has gradually become permanent. The absence of genital pores in Patella, and some Lamellibranchs which make use of the nephridia for the extrusion of their genital products, suggests that the very earliest Mollusca or their forefathers were devoid of genital ducts and pores. In no Mollusca, however, is the nephridium used in the same way as a genital duct as it is in the Chætopoda, the Gephyræa, and the Vertebrata; for the open mouth of the nephridium in Mollusca leads into the pericardial space, and it is not through this space and this mouth that the genital products of any Mollusca enter the nephridium (except perhaps in Neomenia), although it is by this mouth that the genital products enter the nephridium in the former classes above named. Hence the arrangement in Patella, &c., is to be looked upon as a special development from the simpler condition when the Mollusca brought forth by rupture (= schizodinic, from ὠδίς, travail), and not as derived from the common arrangement of adaptation of a nephridium to the genital efferent function (= nephrodinic).[1]

The functional oviduct of Nautilus forms an albuminiparous gland as a diverticulum, which appears to correspond to a dilatation in the male duct, which succeeds the testis itself, and is called the "accessory gland." The male duct has a second dilatation (Needham's sac), and then is produced in the form of a large papilla. In Dibranchs the genital ducts are but little more elaborated. They are ciliated internally. In female Octopoda, in Ommastrephes, and in one male Octopod (*Eledone moschata*) the genital ducts are paired, opening right and left of the anus. But in all other Dibranchs a single genital duct only is developed, viz., that of the left side, and leads from the genital capsule or chamber of the gonad to an asymmetrically-placed pore. In the male Dibranchs the genital duct is coiled and provided with a series of glandular dilatations and receptacles. These are connected with the formation of the spermatophores. In the Siphonopoda the spermatic fluid does not flow as a liquid from the genital pore, but the spermatozoa are made up into little packets before extrusion. In other Mollusca (Pulmonata) and in other animals (Chætopoda) this formation of "sperm-ropes" is known, but in the Siphonopoda it attains its highest development. Exceedingly complicated structures of a cylindrical form (sometimes an inch in length) are formed in the male genital duct by a secretion which embeds and cements together the spermatozoa. They are formed in Nautilus as well as in Dibranchs, the actual manner in which their complicated structure is produced being not easily conjectured. Accessory glands not forming part of the oviduct, but furnishing the material for enclosing the eggs in an elastic envelope, are found as paired structures, opening some way behind the anus in Nautilus (101, *g.n.*) and in the Dibranchs. They are known as the nidamental glands. In the female Sepia they are particularly large and prominent, and are accompanied by a second smaller pair.

Reproduction and Development.—The details of sexual congress and of the actual fertilization of the egg are quite unknown in Nautilus, and imperfectly in the Dibranchs and the Pteropoda. Allusion has already been made to the subject in connexion with the hectocotylized arm. The mature eggs of Nautilus are unknown, as well as the appearance which they present when deposited. In the Dibranchs the eggs are always very large; in some cases the amount of food-yelk infused into the original egg-cell is so great as to give it the size of a large pea. This results in that mode of development which is only known outside this class among the Vertebrata; it is discoblastic. The protoplasm of the fertilized egg-cell segregates to one pole of the egg, and there undergoes cell-division, resulting in the formation of a disc of cleavage cells (fig. 121, (1)) resembling the cicatricula of the hen's egg, which subsequently spreads over and invests the whole egg (fig. 121, (2)). For details of this process we must refer the reader to other works (**45, 46**); but it may here be noted that in addition to the layer of cleavage cells, which consists of more than one stratum of cells in the future embryonic area as opposed to the yelk-sac area, additional cells are formed in the mass of residual yelk apparently by an independent process of segregation, each cell having a separate origin, whence they are termed "autoplasts." The autoplasts eventually form a layer of fusiform cells (fig. 121, (7), *h*; fig. 122, *m*, and fig. 123, *ps*),—the "yelk-membrane" which everywhere rests upon and encloses the residual yelk. The cleavage cells form a single layer on the yelk-sac area and two layers on the embryonic area, an outer layer one cell deep (fig. 122, *ep*), and an inner—the middle layer of the three—which is often thick and many cells deep (fig. 122, *m*). There is great difficulty here in identifying the layers with the three typical layers of other animal embryos, except in regard to the outermost, which corresponds with the epiblast of Vertebrates in many respects. The middle layer, however, gives rise to the nerve-ganglia as well as to the muscles, cœlom, and skeleto-trophic tissues, and to the mid-portion of the alimentary canal with its hepatic diverticula, the liver (see fig. 121, (7) and explanation, where the origin of the mid-gut as a vesicle *r* is seen). It is clearly, therefore, something more than the mesoblast of the Vertebrate, giving rise, as it does, to important organs formed both by epiblast and hypoblast in other animals. Lastly, the yelk-membrane, though corresponding to the Vertebrate hypoblast in position and structure, furnishes no part of the alimentary tract, but disappears when the yelk is completely absorbed. In fact, the developmental phenomena in Sepia, Loligo, and Octopus are profoundly perturbed by the excessive proportion of food-yelk. Balfour has shown

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[1] Cœlomate animals are, according to this nomenclature, either Schizodinic or Porodinic. The Porodinic group is divisible into Nephrodinic and Idiodinic, in the former the nephridium serving as a pore, in the latter a special (ἴδιος) pore being developed. In each of these latter groups the pore may be—(1) devoid of a duct, (2) provided with a duct which is unattached to the gonad and opens into the body-cavity, (3) provided with a duct which fuses with the gonad. The genital ducts of Idiodinic forms may be called Idiogonaducts, as distinguished from the Nephrogonaducts of nephrodinic forms.

that in the chick the orifice of closure of the overspreading blastoderm does not represent the whole of the blastopore, but that this is in part to be sought in the widely-separated primitive streak. The present writer has little doubt that a structure corresponding to the primitive streak of the chick, and lying near the klastic pole, will be found in Sepia and Loligo, and the strange vesicular origin of the mid-gut will be traced to and explained by it.

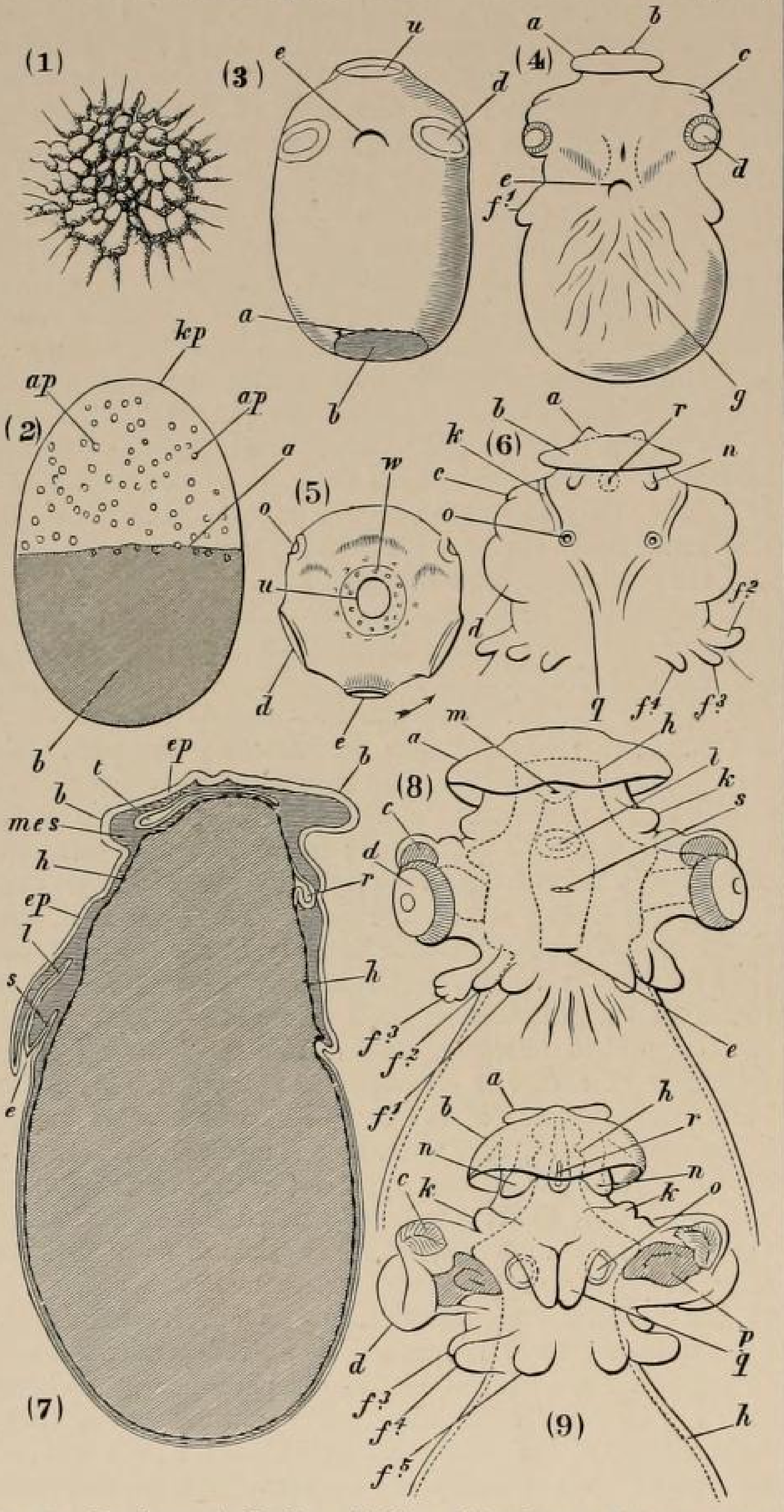

Fig. 121.—Development of Loligo. (1) View of the cleavage of the egg during the first formation of embryonic cells. (2) Lateral view of the egg at a little later stage. *a*, limit to which the layer of cleavage-cells has spread over the egg; *b*, portion of the egg (shaded) as yet uncovered by cleavage-cells; *ap*, the autoplasts; *kp*, cleavage-pole where first cells were formed. (3) Later stage, the limit *a* now extended so as to leave but little of the egg-surface (*b*) unenclosed. The eyes (*d*), mouth (*e*), and mantle-sac (*u*) have appeared. (4) Later stage, anterior surface, the embryo is becoming nipped off from the yelk sac (*g*). (5) View of an embryo similar to (3) from the cleavage-pole or centro-dorsal area. (6) Later stage, posterior surface. (7) Section in a median dorso-ventral and antero-posterior plane of an embryo of the same age as (4). (8) View of the anterior face of an older embryo. (9) View of the posterior face of an embryo of the same age as (8). Letters in (3) to (9):—*a*, lateral fins of the mantle; *b*, mantle-skirt; *c*, supra-ocular invagination to form the "white body"; *d*, the eye; *e*, the mouth; f^1, ^{2}, ^{3}, ^{4}, ^{5}, the five paired processes of the fore-foot; *g*, rhythmically contractile area of the yelk-sac, which is itself a hernia-like protrusion of the median portion of the fore-foot (see fig. 72**); *h*, dotted line showing internal area occupied by yelk (food-material of the egg); *k*, first rudiment of the mid-foot (paired ridges which unite to form the siphon or funnel); *l*, sac of the radula or lingual ribbon; *m*, stomach; *n*, rudiments of the gills (paired ctenidia); *o*, the otocysts,—a pair of invaginations of the surface of the mid-foot; *p*, the optic ganglion; *q*, the distal portion of the ridges which form the siphon or mid-foot, *k* being the basal portion of the same structure; *r*, the vesicle-like rudiment of the intestine formed independently of the parts connected with the mouth, *s*, *k*, *m*, and without invagination; *s*, rudiment of the salivary glands; *t* in (7), the shell-sac at an earlier stage open (see fig. 122), now closed up; *u*, the open shell-sac formed by an uprising ring-like growth of the centro-dorsal area; *w* in (5), the mantle-skirt commencing to be raised up around the area of the shell-sac. In (7) *mes* points to the middle cell-layer of the embryo, *ep* to the outer layer, and *h* to the deep layer of fusiform cells which separates everywhere the embryo from the yelk or food-material lying within it. (Original.)

Leaving this difficult question of the cell-layers of the embryo, we would draw the reader's attention to the series of sketches representing the semi-transparent embryo of Loligo, drawn in fig. 121. When the cleavage cells have nearly enclosed the yelk, the upper or embryonic area shows the rudiments of the centro-dorsal mantle-sac or pen-sac, the mouth, the paired optic pits, and the paired otic pits (fig. 121, (3), (5)). The eye-pits close up (fig. 119), the orifice of the mantle-sac narrows, and its margin becomes raised and freely produced as mantle-skirt; at the same time an hour-glass-like pinching in of the whole embryo commences, separating the embryo proper from the so-called yelk-sac (fig. 121, (4)). Around the "waist" of constriction, pair by pair, ten lobes arise (fig. 121, (8)),—the arms of the fore-foot. It now becomes obvious that the yelk-sac is but the median surface of the fore-foot bulged out inordinately by food-yelk, just as the hind region of the foot is in the embryo slug (see fig. 72**, and explanation). Just as in the slug, this dilated yelk-holding foot is rhythmically contractile, and pulsates steadily over the area *g* in fig. 121, (4). At this stage, and long subsequently, the mouth of the young Cephalopod is in no way surrounded by the fore-foot, but lies well above its nascent lobes (*e* in fig. 121). Subsequently it sinks, as it were, between the right and left most anterior pair of the series, which grow towards one another and fuse above it, and leave no trace of their original position and relations. Fig. 121, (6) gives a view of the postero-dorsal surface of an embryo, in which the important fact is seen of the formation of the funnel or siphon by the union of two pieces (*q*), which grow up each independently, one right and one left, like the sides of the siphon of Nautilus or the swimming lobes of a Pteropod, and subsequently come together, as shown in (9), where the same letter *q* indicates the same part. The explanations of figs. 121 and 123 are given very full, and here, therefore, we shall only allude to two additional points. A curious mass of tissue of unknown significance occurs in the orbit of Dibranchs, known as the white body (*w* in fig. 120). A strongly-marked invagination just above the orbit is a very prominent feature in the embryo of Loligo, Sepia, and Octopus, and appears to give rise to this so-called white body. This invaginated portion of the outer cell-layer is seen in fig. 121, (8) and (9), lettered *c*; in fig. 123, A and B, it is lettered *wb*.

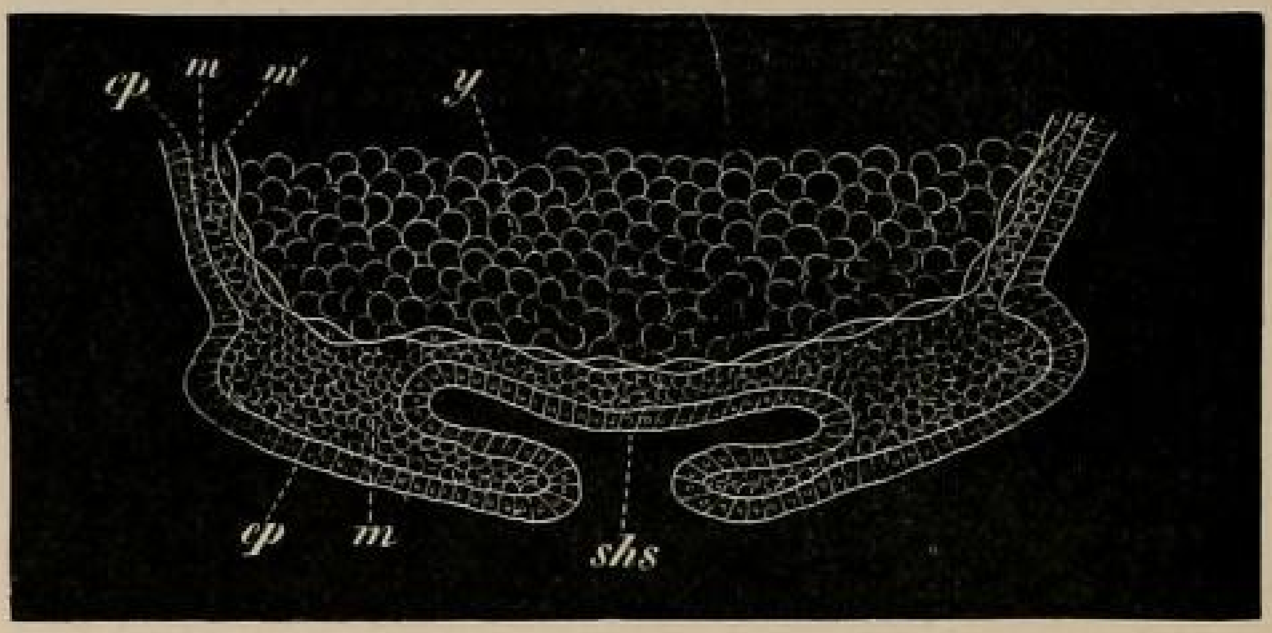

Fig. 122.—Section through the still open shell-sac occupying the centro-dorsal area of an embryo of Loligo; the position is inverted as compared with fig. 121 (3) and (7). *ep*, outer cell-layer; *m*, middle cell-layer; *m′*, deep cell-layer of fusiform cells; *y*, the granular yelk or food-material of the egg; *shs*, the still open shell-sac. (From Lankester.)

Lastly, in fig. 123, A, the origin of the optic nerve-ganglion *ng* from the cells of the middle layer should be especially noticed. In some other Molluscs the nerve-ganglia have been definitely traced to the outer cell-layer, whilst in some Gastropods, according to Bobretzky, they originate, as here shown, for Loligo.

The egg-coverings of the Dibranchiate are very complete. Argonauta and Octopus deposit each egg in a firm oval case, thin and transparent, which has a long stalk by which (in Octopus) the egg is fixed in company with two or three hundred others to some foreign object. Sepia encloses each egg in a thick envelope of many layers resembling india-rubber. Loligo encloses many rows of eggs in a copious tough jelly, and affixes a dozen or twenty such egg-strings to one spot. Sepia and Loligo desert their eggs when laid. The female Octopus most jealously guards them, building a nest of stones and incubating. Argonauta carries hers with her in a special brood-holding shell.

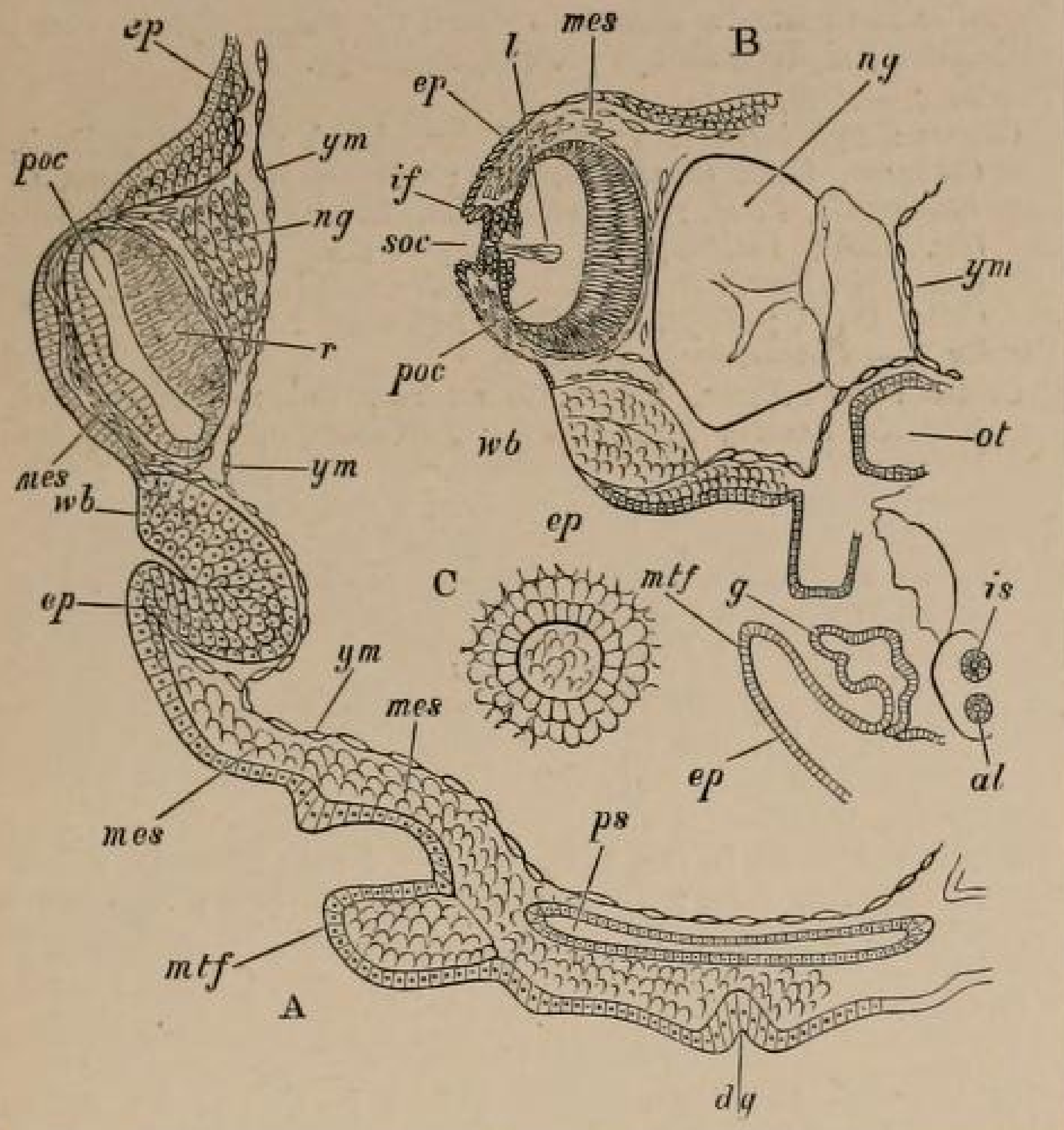

FIG. 123.—Right and left sections through embryos of Loligo. A. Same stage as fig. 121 (4). B. Same stage as fig. 121 (8); only the left side of the sections is drawn, and the food-material which occupies the space internal to the membrane *ym* is omitted. *al*, rectum; *is*, ink-sac; *ep*, outer cell-layer; *mes*, middle cell-layer; *ym*, deep cell-layer of fusiform cells (yelk-membrane); *ng*, optic nerve-ganglion; *ot*, otocyst; *wb*, the "white body" of the adult ocular capsule forming as an invagination of the outer cell-layer; *mtf*, mantle-skirt; *g*, gill; *ps*, pen-sac or shell-sac, now closed; *dg*, dorsal groove; *poc*, primitive optic vesicle, now closed (see fig. 119); *l*, lens; *r*, retina; *soc*, second or anterior optic chamber still open; *if*, iridean folds. C. The primitive invagination to form one of the otocysts, as seen in fig. 121 (5) and (6). (After Lankester.)

The development of the Pteropoda, so far as is known, presents no points of contact with that of the Siphonopoda rather than with that of the Gastropoda, owing to the fact that in them the egg has not an excess of food-yelk. Consequently, we find typical trochosphere and veliger larvæ among the Thecosomata (fig. 8, C, and fig. 81), whilst the isolated observation of Gegenbaur has made known very remarkable larvæ referable to the Gymnosomata, and with little doubt to Pneumodermon (fig. 84). The former set of larvæ are sufficient to demolish once for all the view which has been entertained by some zoologists, viz., that the velar disc of the veliger larva is the same thing as the pteropodial lobes of the mid-foot of Pteropoda. The latter larvæ are of importance in showing that, as in embryo Siphonopods so in embryo Pteropods, the sucker-bearing lobes of the fore-foot are truly podial structures, and only embrace the head and surround the mouth as the result of late embryonic growth.

BRANCH B.—*LIPOCEPHALA.*

Characters.—Mollusca with the head region undeveloped. No cephalic eyes are present; the buccal cavity is devoid of biting, rasping, or prehensile organs. The animal is sessile, or endowed with very feeble locomotive powers. The Lipocephala comprise but one class, the Lamellibranchia, also known as Elatobranchia and Conchifera.

Class **LAMELLIBRANCHIA.**

Characters.—Lipocephala in which the archaic BILATERAL SYMMETRY of the Mollusca is usually fully retained, and raised to a dominant feature of the organization by the lateral compression of the body and the development of the shell as two bilaterally symmetrical plates or valves covering each one side of the animal. The FOOT is commonly a simple cylindrical or ploughshare-shaped organ, used for boring in sand and mud, and more rarely presents a crawling disc similar to that of Gastropoda; in some forms it is aborted. The paired CTENIDIA are very greatly developed right and left of the elongated body, and form the most prominent organ of the group. Their function is chiefly not respiratory but nutritive, since it is by the currents produced by their ciliated surface that food-particles are brought to the feebly-developed mouth and buccal cavity.

The Lamellibranchia present as a whole a somewhat uniform structure, so that, although they are very numerous, it is not possible to divide them into well-marked sub-classes or sections, and orders. The chief points in which they vary are—(1) in the structure of the ctenidia or branchial plates; (2) in the presence of one or of two chief muscles, the fibres of which run across the animal's body from one valve of the shell to the other (adductors); (3) in the greater or less elaboration of the posterior portion of the mantle-skirt so as to form a pair of tubes, by one of which water is introduced into the sub-pallial chamber, whilst by the other it is expelled; (4) in the perfect or deficient symmetry of the two valves of the shell and the connected soft parts, as compared with one another; (5) in the development of the foot as a disc-like crawling organ (Arca, Nucula, Pectunculus, Trigonia, Lepton, Galeomma), as a simple plough-like or tongue-shaped organ (Unionacea, &c.), as a re-curved saltatory organ (Cardium, &c.), as a long burrowing cylinder (Solenacea, &c.), or its partial (Mytilacea) or even complete abortion (Ostracea).

The essential Molluscan organs are, with these exceptions, uniformly well developed. The MANTLE-SKIRT is always long, and hides the rest of the animal from view, its dependent margins meeting in the middle line below the ventral surface when the animal is retracted; it is, as it were, slit in the median line before and behind so as to form two flaps, a right and a left; on these the right and the left calcareous valves of the shell are borne respectively, connected by an uncalcified part of the shell called the ligament. In many embryo Lamellibranchs a centro-dorsal PRIMITIVE SHELL-GLAND or follicle has been detected (figs. 8 and 151). The MOUTH lies in the median line anteriorly, the ANUS in the median line posteriorly.

Both CTENIDIA right and left are invariably present, the axis of each taking origin from the side of the body as in the schematic archi-Mollusc (see fig. 1 and fig. 131). A pair of NEPHRIDIA opening right and left, rather far forward on the sides of the body, are always present. Each opens by its internal extremity into the pericardium. A pair of GENITAL APERTURES, connected by genital ducts with the paired gonads, are found right and left near the nephridial pores, except in a few cases where the genital duct joins that of the nephridium (Spondylus). The sexes are often, but not always, distinct. No accessory glands or copulatory organs are ever present in Lamellibranchs. The ctenidia often act as brood-pouches.

A dorsal contractile HEART, with symmetrical right and left auricles (fig. 143, A) receiving aerated blood from the ctenidia and mantle-skirt, is present, being unequally developed only in those few forms which are inequivalve. The typical **PERICARDIUM** is well developed. It appears, as in other Mollusca, not to be a blood-space although developed from the cœlom, and it communicates with the exterior by the pair of nephridia. As in Cephalopoda (and possibly other Mollusca) water can be introduced through the nephridia into this space. The **ALIMENTARY CANAL** keeps very nearly to the median vertical plane whilst exhibiting a number of flexures and loopings in this plane. A pair of large glandular outgrowths, the so-called "liver" or great digestive gland, exists as in other Molluscs. A pair of pedal **OTOCYSTS**, and a pair of **OSPHRADIA** at the base of the gills, appear to be always present. A typical **NERVOUS SYSTEM** is present (fig. 144), consisting of a cerebro-pleuro-visceral ganglion-pair, united by connectives to a pedal ganglion-pair and an osphradial ganglion-pair (parieto-splanchnic).

A special cæcum connected with the pharynx is sometimes found, containing a tough flexible cylinder of transparent cartilaginous appearance and unknown significance, called the "crystalline style" (Mactra), which possibly represents the radular sac of Glossophora. In many Lamellibranchs a gland is found on the hinder surface of the foot in the mid line, which secretes a substance which sets into the form of threads—the so-called "byssus"—by means of which the animal can fix itself. Sometimes this gland is found in the young and not in the adult (Anodon, Unio, Cyclas). In some Lamellibranchs (Pecten, Spondylus, Pholas, Mactra, Tellina, Pectunculus, Galeomma, &c.), although cephalic eyes are always absent, special eyes are developed on the free margin of the mantle-skirt, apparently by the modification of tentacles which are commonly found there (fig. 145). The existence of pores in the foot and elsewhere in Lamellibranchia by which liquid can pass into and out of the vascular system, although asserted as in the case of other Mollusca, appears to be improbable. It has yet to be shown by satisfactory microscopic sections that the supposed pores are anything but epidermal glands.

The Lamellibranchia live chiefly in the sea, some in fresh waters. A very few have the power of swimming by opening and shutting the valves of the shell (Pecten, Lima); most can slowly crawl or rapidly burrow; others are, when adult, permanently fixed to stones or rocks either by the shell or the byssus. In development some Lamellibranchia pass through a free-swimming trochosphere stage with præoral ciliated band; other fresh-water forms which carry the young in brood-pouches formed by the ctenidia have suppressed this larval phase.

The following classification and enumeration of genera are based primarily upon the characters of the adductor muscles. The Heteromya and Monomya must be conceived of as derived from forms resembling such Gastropodous Isomya as Nucula and Trigonia, which undoubtedly are the nearest living representatives of the ancestral Lipocephala, and bring us nearest to the other branch of the Mollusca, the Glossophora.

Order 1.—**Isomya.**

Character.—Anterior and posterior adductor muscles of approximately equal size.

Sub-order 1.—*Integripallia.*

Characters.—Marginal attachment of the mantle to the shell not inflected to form a sinus; siphons not developed in some, present in most.

Family 1.—*Arcacea.*

Genera: *Arca*, L. (fig. 132); *Cucullæa*, Lam.; *Pectunculus*, Lam.; *Limopsis*, Sassi; *Nucula*, Lam. (fig. 134); *Isoarca*, Münster; *Leda*, Schu.; *Yoldia*, Möll.; *Solenella*, Sowerby, &c.

Family 2.—*Trigoniacea.*

Genera: *Trigonia*, Brug.; *Axinus*, Sow.; *Lyrodesma*, Conrad.

Family 3.—*Unionacea.*

Genera: *Unio*, Retz.; *Castalia*, Lam.; *Anodon*, Cuv. (figs. 124, &c.); *Iridina*, Lam.; *Mycetopus*, d'Orb., &c.

Family 4.—*Lucinacea.*

Genera: *Lucina*, Brug.; *Corbis*, Cuv.; *Diplodonta*, Brown; *Kellia*, Turton; *Montacuta*, Turton; *Lepton*, Turton; *Galeomma*, Turton; *Astarte*, Sow.; *Crassatella*, Lam.; *Cardinia*, Ag.; *Cardita*, Brug., &c.

Family 5.—*Cyprinacea.*

Genera: *Tridacna*, Da C.; *Chama*, L.; *Dimya*, Ron.; *Diceras*, Lk.; *Isocardia*, Lam.; *Hippopodium*, Sow.; *Cardium*, L.; *Corbicula*, Meg.; *Cyrena*, Lk.; *Cyclas*, Brug. (fig. 146); *Pisidium*, Pfr. (figs. 148-153); *Cyprina*, Lam., &c.

Sub-order 2.—*Sinupallia.*

Characters.—Marginal attachment of the mantle to the shell inflected so as to form a sinus into which the pallial siphons can be withdrawn; siphons always present, and large.

Family 6.—*Veneracea.*

Genera: *Cypricardia*, Lam.; *Tapes*, Megl.; *Cyclina*, Desh.; *Cytherea*, Lam. (figs. 125, &c.); *Chione*, Megl.; *Venus*, L.; *Lucinopsis*, F. H.; *Sanguinolaria*, Lam.; *Psammobia*, Lam. (fig. 130); *Tellina*, L.; *Donax*, L.; *Scrobicularia*, Schu.; *Cumingia*, Sow.; *Rangia*, Dsml.; *Mactra*, L. (fig. 140); *Trigonella*, Da C.; *Vaganella*, Gr.; *Lutraria*, Lam.

Family 7.—*Myacea.*

Genera: *Myochama*, Stb.; *Chamostrea*, Rois; *Pandora*, Sol.; *Thracia*, Leach; *Thetis*, Sow.; *Pholadomya*, Sow.; *Corbula*, Brug.; *Mya*, Lam.; *Saxicava*, Fleur; *Panopæa*, Ad.; *Glycimeris*, Lam.; *Siliqua*, Mhlf., &c.; *Solen*, L.

Family 8.—*Pholadacea.*

Genera: *Clavagella*, Lam.; *Aspergillum*, Lam. (figs. 128, 129); *Humphreyia*, Gr.; *Pholas*, L.; *Pholadidea*, Turt.; *Teredo*, L.; *Teredina*, Lam.; *Furcella*, Oken, &c.

Order 2.—**Heteromya.**

Characters.—Anterior adductor (pallial adductor) much smaller than the posterior adductor (pedal adductor); siphons rarely present.

Family 1.—*Mytilacea.*

Genera: *Mytilus*, L. (fig. 133); *Modiola*, Lam.; *Crenella*, Brown; *Lithodomus*, Cuv.; *Dreissena*, Ben. (fig. 136); *Modiolarca*, Gr., &c.

Family 2.—*Mulleriacea.*

Genera: *Aetheria*, Lam.; *Mulleria*, Fér.

Order 3.—**Monomya.**

Characters.—Anterior adductor absent in the adult; siphons never developed.

Family 1.—*Aviculacea.*

Genera: *Cardiola*, Brdp.; *Avicula*, Kl.; *Malleus*, Lam.; *Inoceramus*, Sow.; *Crenatula*, Lam.; *Perna*, Brug., &c.

Family 2.—*Ostracea.*

Genera: *Ostrea*, L. (fig. 6); *Anomia*, L.; *Spondylus*, L.; *Plicatula*, Lam.; *Vulsella*, Lam.; *Lima*, Brug.; *Pecten*, L.; *Hiunites*, Dfr., &c.

Further Remarks on the Lamellibranchia.—The Lamellibranchia are the only members of the Lipocephalous branch of Mollusca existing at the present day; and we must suppose that, whilst on the one hand the earliest Glossophorous forms were developing from the archi-Mollusca by the elaboration of the buccal apparatus, the bivalved sessile Lamellibranchs were developing in another direction from univalve cephalophorous ancestors. The large bilobed mantle-flap with its pair of shells covering in the whole animal, the current-producing largely-expanded ctenidia, and the reduced cephalic region are characters which go hand in hand, and were simultaneously acquired, each being related to the development of the others. Unless the "crystalline style" of Lamellibranchs is to be considered as the rudiment of the "radular sac" of Glossophora, as suggested by Balfour, there is no indication whatever that the ancestors of the Lamellibranchia had acquired a representative of the buccal apparatus—so highly developed in Glossophora—before diverging from the archi-Mollusca; that is to say, the common ancestors of the two great branches of Mollusca presented the distinctive character of neither branch—they had not an aborted cephalic region, and they had not a lingual ribbon.

As an example of the organization of a Lamellibranch, we shall review the structure of the Common Pond-Mussel (*Anodonta cygnea*), comparing its structure with those of other Lamellibranchia. The Swan Mussel has superficially a perfectly-developed bilateral symmetry. The left side of the animal is seen as when removed from its shell in fig. 124 (1). The valves of the shell have been removed by severing their adhesions to the muscular areæ *h*, *i*, *k*, *l*, *m*, *u*.

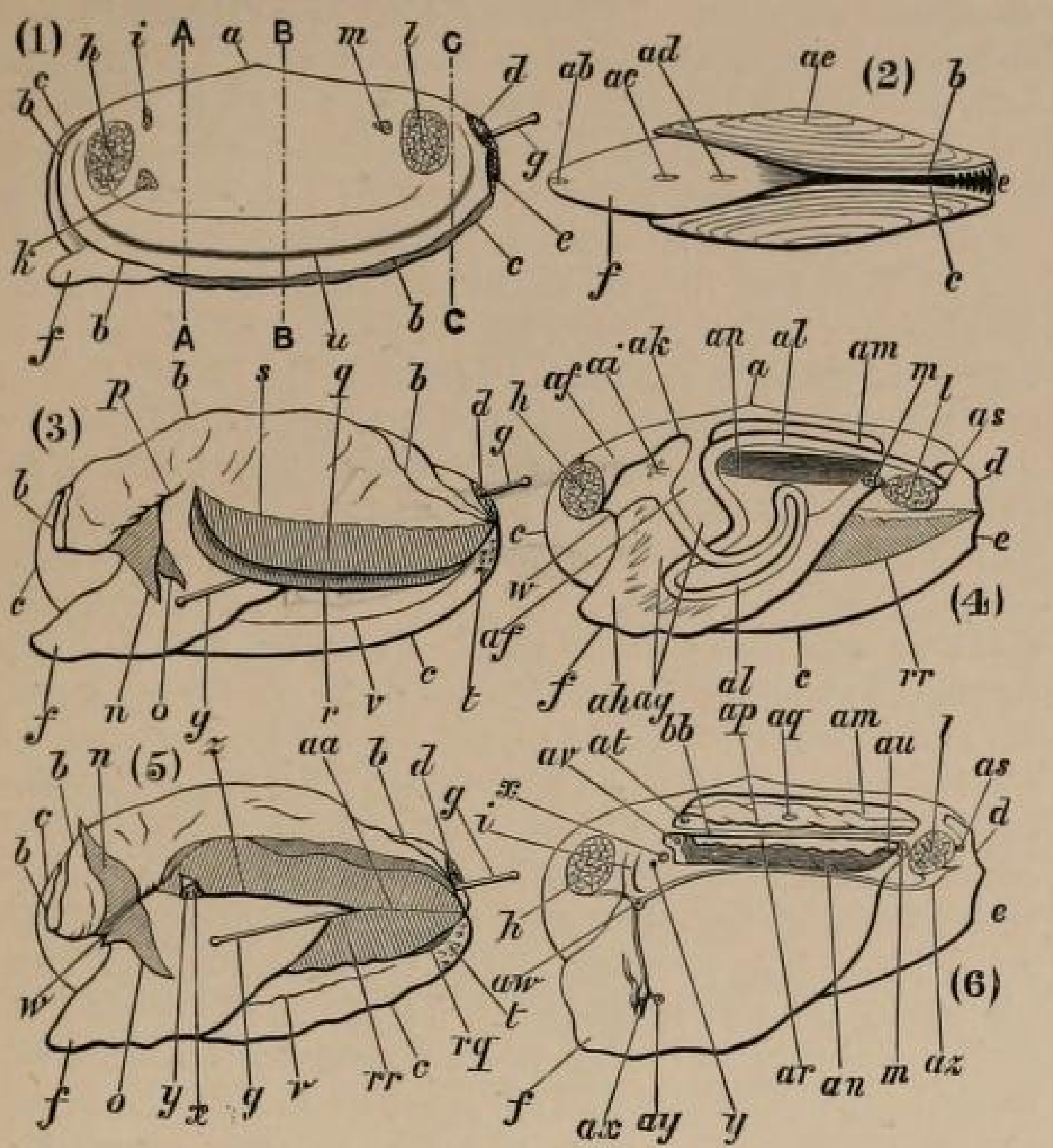

FIG. 124.—Diagrams of the external form and anatomy of *Anodonta cygnea*, the Pond-Mussel; in all the figures the animal is seen from the left side, the centro-dorsal region uppermost, as in the drawings of fig. 75, which compare. (1) Animal removed from its shell, a probe *g* passed into the sub-pallial chamber through the excurrent siphonal notch. (2) View from the ventral surface of an Anodon with its foot expanded and issuing from between the gaping shells. (3) The left mantle-flap reflected upwards so as to expose the sides of the body. (4) Diagrammatic section of Anodon to show the course of the alimentary canal. (5) The two gill-plates of the left side reflected upwards so as to expose the fissure between foot and gill where the probe *g* passes. (6) Diagram to show the positions of the nerve-ganglia, heart, and nephridia.

Letters in all the figures as follows:—*a*, centro-dorsal area; *b*, margin of the left mantle-flap; *c*, margin of the right mantle-flap; *d*, excurrent siphonal notch of the mantle margin; *e*, incurrent siphonal notch of the mantle margin; *f*, foot; *g*, probe passed into the superior division of the sub-pallial chamber through the excurrent siphonal notch, and issuing by the side of the foot into the inferior division of the sub-pallial chamber; *h*, anterior (pallial) adductor muscle of the shells; *i*, anterior retractor muscle of the foot; *k*, protractor muscle of the foot; *l*, posterior (pedal) adductor muscle of the shells; *m*, posterior retractor muscle of the foot; *n*, anterior labial tentacle; *o*, posterior labial tentacle; *p*, base-line of origin of the reflected mantle-flap from the side of the body; *q*, left external gill-plate; *r*, left internal gill-plate; *rr*, inner lamella of the right inner gill-plate; *rg*, right outer gill-plate; *s*, line of concrescence of the outer lamella of the left outer gill-plate with the left mantle-flap; *t*, pallial tentacles; *u*, the thickened muscular pallial margin which adheres to the shell and forms the pallial line of the left side; *v*, that of the right side; *w*, the mouth; *x*, aperture of the left organ of Bojanus (nephridium) exposed by cutting the attachment of the inner lamella of the inner gill-plate; *y*, aperture of the genital duct; *z*, fissure between the free edge of the inner lamella of the inner gill-plate and the side of the foot, through which the probe *g* passes into the upper division of the sub-pallial space; *aa*, line of concrescence of the inner lamella of the right inner gill-plate with the inner lamella of the left inner gill-plate; *ab*, *ac*, *ad*, three pit-like depressions in the median line of the foot supposed by some writers to be pores admitting water into the vascular system; *ae*, left shell valve; *af*, space occupied by liver; *ag*, space occupied by gonad; *ah*, muscular substance of the foot; *ai*, duct of the liver on the wall of the stomach; *ak*, stomach; *al*, rectum traversing the ventricle of the heart; *am*, pericardium; *an*, glandular portion of the left nephridium; *ap*, ventricle of the heart; *aq*, aperture by which the left auricle joined the ventricle; *ar*, non-glandular portion of the left nephridium; *as*, anus; *at*, pore leading from the pericardium into the glandular sac of the left nephridium; *au*, pore leading from the glandular into the non-glandular portion of the left nephridium; *av*, internal pore leading from the non-glandular portion of the left nephridium to the external pore *x*; *aw*, left cerebro-pleuro-visceral ganglion; *ax*, left pedal ganglion; *ay*, left otocyst; *az*, left olfactory ganglion (parieto-splanchnic); *bb*, floor of the pericardium separating that space from the non-glandular portion of the nephridia.

The free edge of the left half of the mantle-skirt *b* is represented as a little contracted in order to show the exactly similar free edge of the right half of the mantle-skirt *c*. These edges are not attached to, although they touch, one another; each flap (right or left) can be freely thrown back in the way which has been carried out in fig. 124, (3) for that of the left side. This is not always the case with Lamellibranchs; there is in the group a tendency for the corresponding edges of the mantle-skirt to fuse together by concrescence, and so to form a more or less completely closed bag, as in the Scaphopoda (Dentalium). In this way the notches *d*, *e* of the hinder part of the mantle-skirt of Anodon are in the Siphonate forms converted into two separate holes, the edges of the mantle being elsewhere fused together along this hinder margin. Further than this, the part of the mantle-skirt bounding the two holes is frequently drawn out so as to form a pair of tubes which project from the shell (figs. 130, 141). In such Lamellibranchs as the oysters, scallops, and many others which have the edges of the mantle-skirt quite free, there are numerous tentacles upon those edges. In Anodon these pallial tentacles are confined to a small area surrounding the inferior siphonal notch (fig. 124, (3), *t*).

The centro-dorsal point *a* of the animal of Anodonta (fig. 124, (1)) is called the umbonal area; the great anterior muscular surface *h* is that of the anterior adductor muscle, the posterior similar surface *i* is that of the posterior adductor muscle; the long line of attachment *u* is the simple "pallial muscle,"—a thickened ridge which is seen to run parallel to the margin of the mantle-skirt in this Lamellibranch. In some of the Siphonate Isomya, which are hence termed "Sinupallia," the pallial muscle is not simple but deeply incurved at the posterior region so as to allow of the large pallial siphons being retracted within the shell or expanded at will (fig. 127, and figs. 140, 141).

It is the approximate equality in the size of the anterior and posterior adductor muscles which has led to the name Isoyma for the group to which Anodon belongs. The hinder adductor muscle may be considered as representing morphologically the transverse fibres of the root of the foot of Nautilus by which it adheres to its shell (fig. 91, *k*), the annular muscular area of Patella (fig. 27, *c*), and the columella muscle of the Gastropods generally. It is always large in Lamellibranchs, but the anterior adductor may be very small (Heteromya), or absent altogether (Monomya). The anterior adductor muscle is in front of the mouth and alimentary tract altogether, and must be regarded as a special and peculiar development of the median anterior part of the mantle-flap in Heteromya and Isomya. Amongst those Lamellibranchs which have only a posterior adductor (Monomya), it is remarkable that the oyster has been found (by Huxley) to possess, when the young shells and muscles first develop, a well-marked anterior adductor as well as a posterior one. Accordingly there is ground for supposing

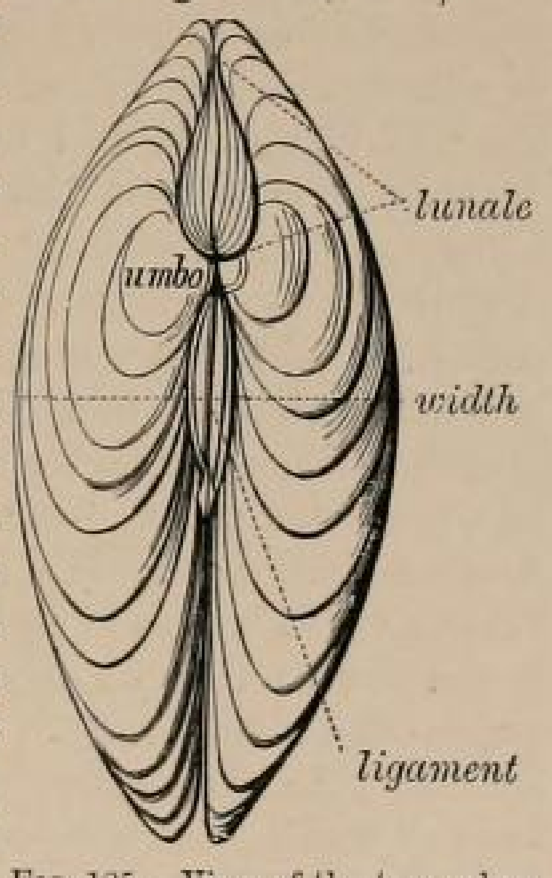

FIG. 125.—View of the two valves of the shell of Cytherea (one of the Sinupalliate Isomya), from the dorsal aspect.

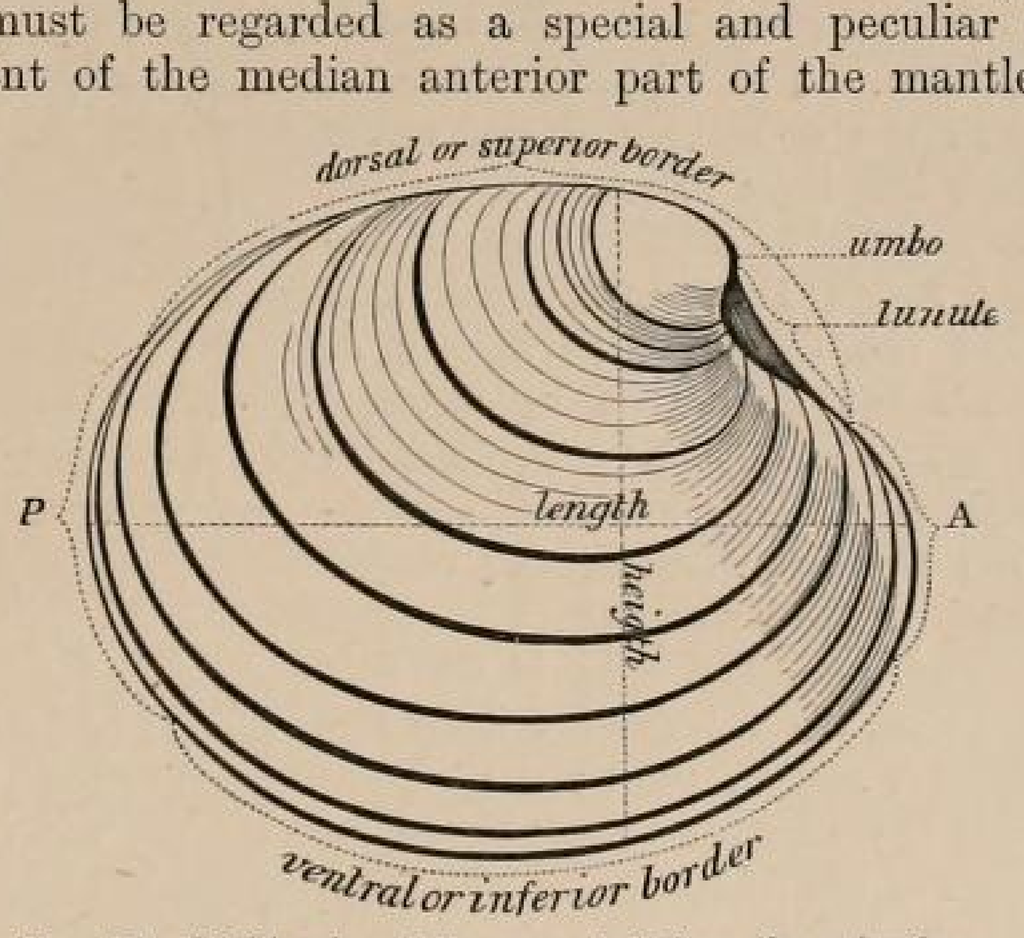

FIG. 126.—Right valve of the same shell from the outer face.

that the Monomya have been developed from Isomya-like ancestors, and have lost by atrophy their anterior adductor. The single adductor muscle of the Monomya is separated by a difference of fibre into two portions, but neither of these can be regarded as possibly representing the anterior adductor of the other Lamellibranchs. One of these portions is more ligamentous, and serves to keep the two shells constantly attached to one another, whilst the more fleshy portion serves to close the shell rapidly when it has been gaping.

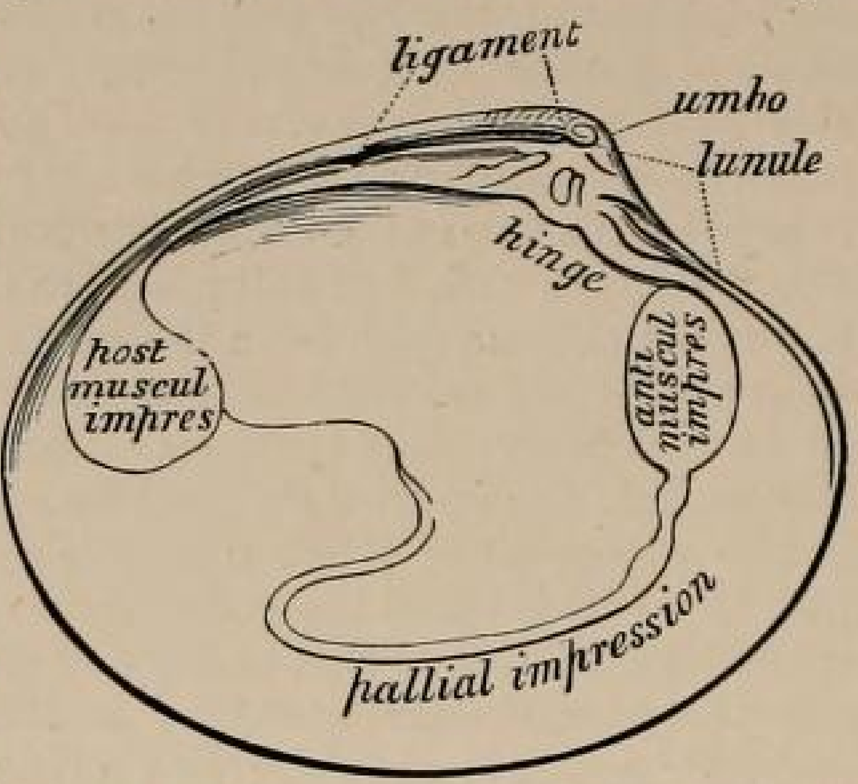

Fig. 127.—Left valve of the same shell from the inner face. (Figs. 125, 126, 127 from Owen.)

In removing the valves of the shell from an Anodon, it is necessary not only to cut through the muscular attachments of the body-wall to the shell but to sever also a strong elastic ligament, or spring resembling india-rubber, joining the two shells about the umbonal area. The shell of Anodon does not present these parts in the most strongly marked condition, and accordingly our figures (figs. 125, 126, 127) represent the valves of the Sinupalliate genus Cytherea. The corresponding parts are recognizable in Anodon. Referring to the figures (125, 126) for an explanation of terms applicable to the parts of the valve and the markings on its inner surface—corresponding to the muscular area which we have already noted on the surface of the animal's body—we must specially note here the position of that denticulated thickening of the dorsal margin of the valve which is called the hinge (fig. 127). By this hinge one valve is closely fitted to the other. Below this hinge each shell becomes concave, above it each shell rises a little to form the umbo, and it is into this ridge-like upgrowth of each valve that the elastic ligament or spring is fixed (fig. 127). As shown in the diagram (fig. 127*) representing a transverse section of the two valves of a Lamellibranch, the two shells form a double lever, of which the toothed-hinged is the fulcrum. The adductor muscles placed in the concavity of the shells act upon the long arms of the lever at a mechanical advantage; their contraction keeps the shells shut, and stretches the ligament or spring *h*. On the other hand, the ligament *h* acts upon the short arm formed by the umbonal ridge of the shells; whenever the adductors relax, the elastic substance of the ligament contracts, and the shells gape. It is on this account that the valves of a dead Lamellibranch always gape; the elastic ligament is no longer counteracted by the effort of the adductors. The state of closure of the valves of the shell is not, therefore, one of rest; when it is at rest—that is, when there is no muscular effort—the valves of a Lamellibranch are slightly gaping, and are closed by the action of the adductors when the animal is disturbed. The ligament is simple in Anodon; in many Lamellibranchs it is separated into two layers, an outer and an inner (thicker and denser). That the condition of gaping of the shell-valves is essential to the life of the Lamellibranch appears from the fact that food to nourish it, water to aerate its blood, and spermatozoa to fertilize its eggs, are all introduced into this gaping chamber by currents of water, which are set going by the highly-developed ctenidia. The current of water enters into the sub-pallial space at the spot marked *e* in fig. 124, (1), and, after passing as far forward as the mouth *w* in fig. 124, (5), takes an outward course and leaves the sub-pallial space by the upper notch *d*. These notches are known in Anodon as the afferent and efferent siphonal notches respectively, and correspond to the long tube-like afferent inferior and efferent superior "siphons" formed by the mantle in many other Lamellibranchs (fig. 130).

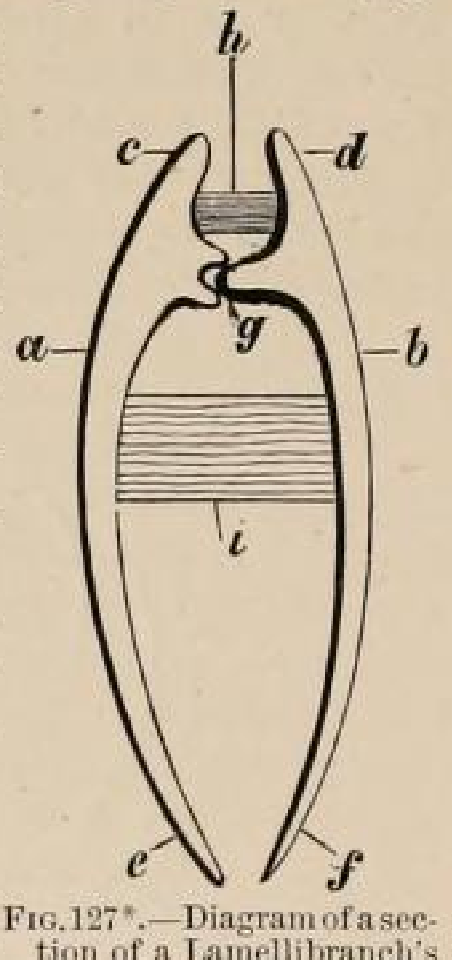

Fig. 127*.—Diagram of a section of a Lamellibranch's shells, ligament, and adductor muscle. *a*, *b*, right and left valves of the shell; *c*, *d*, the umbones or short arms of the lever; *e*, *f*, the long arms of the lever; *g*, the hinge; *h*, the ligament; *i*, the adductor muscle.

Whilst the valves of the shell are equal in Anodon we find in many Lamellibranchs (Ostræa, Chama, Corbula, &c.) one valve larger, and the other smaller and sometimes flat, whilst the larger shell may be fixed to rock or to stones (Ostræa, &c.). A further variation consists in the development of additional shelly plates upon the dorsal line between the two large valves (Pholadidæ). In *Pholas dactylus* we find a pair of umbonal plates, a dors-umbonal plate and a dorsal plate. It is to be remembered that the whole of the cuticular hard product produced on the dorsal surface and on the mantle-flaps is to be regarded as the "shell," of which a median band-like area, the ligament, usually remains uncalcified, so as to result in the production of two valves united by the elastic ligament. But the shelly substance does not always in boring forms adhere to this form after its first growth. In Aspergillum the whole of the tubular mantle area secretes a continuous shelly tube, although in the young condition two valves were present. These are seen (fig. 129) set in the firm substance of the adult tubular shell, which has even replaced the ligament, so that the tube is complete. In Teredo a similar tube is formed as the animal elongates (boring in wood), the original shell-valves not adhering to it but remaining movable and provided with a special muscular apparatus in place of a ligament.

Fig. 128.

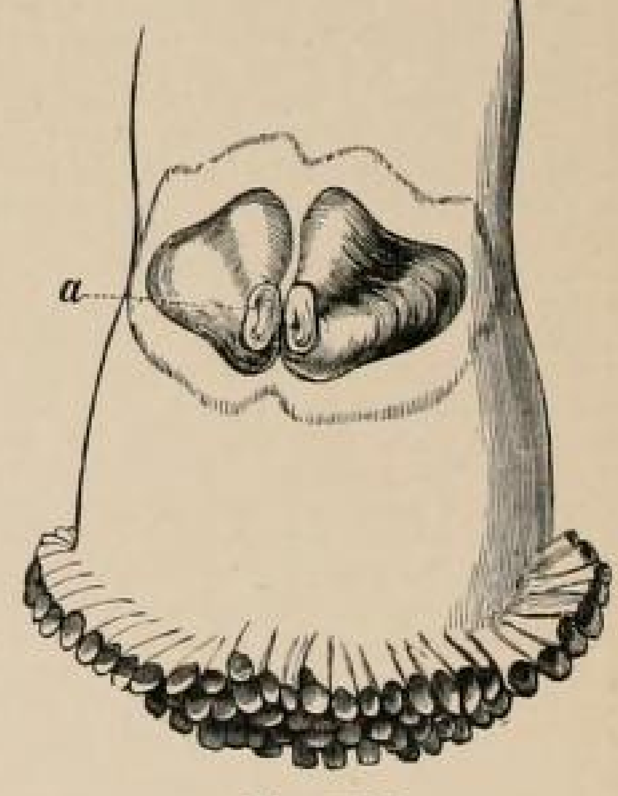

Fig. 129.

Fig. 128.—Shell of *Aspergillum vaginiferum* (from Owen).
Fig. 129.—Shell of *Aspergillum vaginiferum* to show the original valves *a*, now embedded in a continuous calcification of tubular form (from Owen).

Let us now examine the organs which lie beneath the mantle-skirt of Anodon, and are bathed by the current of water which circulates through it. This can be done by lifting up and throwing back the left half of the mantle-skirt as is represented in fig. 124, (3). We thus expose the plough-like foot (*f*), the two left labial tentacles, and the two left gill-plates or left ctenidium. In fig. 124, (5), one of the labial tentacles *n* is also thrown back so as to show the mouth *w*, and the two left gill-plates are reflected so as to show the gill-plates of the right side (*rr*, *rq*) projecting behind the foot, the inner or median plate of each side being united by concrescence to its fellow of the opposite side along a continuous line (*aa*). The left inner gill-plate is also snipped so as to show the subjacent orifices of the left nephridium *x*, and of the genital gland (testis or ovary) *y*. The foot thus exposed in Anodon is a simple muscular tongue-like organ. It can be protruded between the flaps of the mantle (fig. 124, (1), (2)) so as to issue from the shell, and by its action the Anodon can slowly crawl, or burrow in soft mud or sand. It has been supposed that water is taken into the blood-vessels of the Anodon through pores in the foot, and in spite of opposition this view is still maintained (Griesbach, **47**). In fig. 124, (2) the letters *ab*, *ac*, *ad*, point to three pit-like depressions, supposed by Griesbach to be pores leading into the blood-system. According to Carrière (**48**) these pits are nothing but irregularities of the surface; in some cases they are the entrances to ramified glands. Other Lamellibranchs may have a larger foot relatively than has Anodon. In Arca it has a sole-like surface. In Arca too and many others it carries a byssus-forming gland and a byssus-cementing gland. In the Cockles, in Cardium, and in Trigonia, it is capable of a sudden stroke, which causes the animal to jump when out of the water, in the latter genus to a height of four feet. In Mytilus the foot is reduced to little more than a tubercle carrying the apertures of these glands. In the Oyster it is absent altogether.

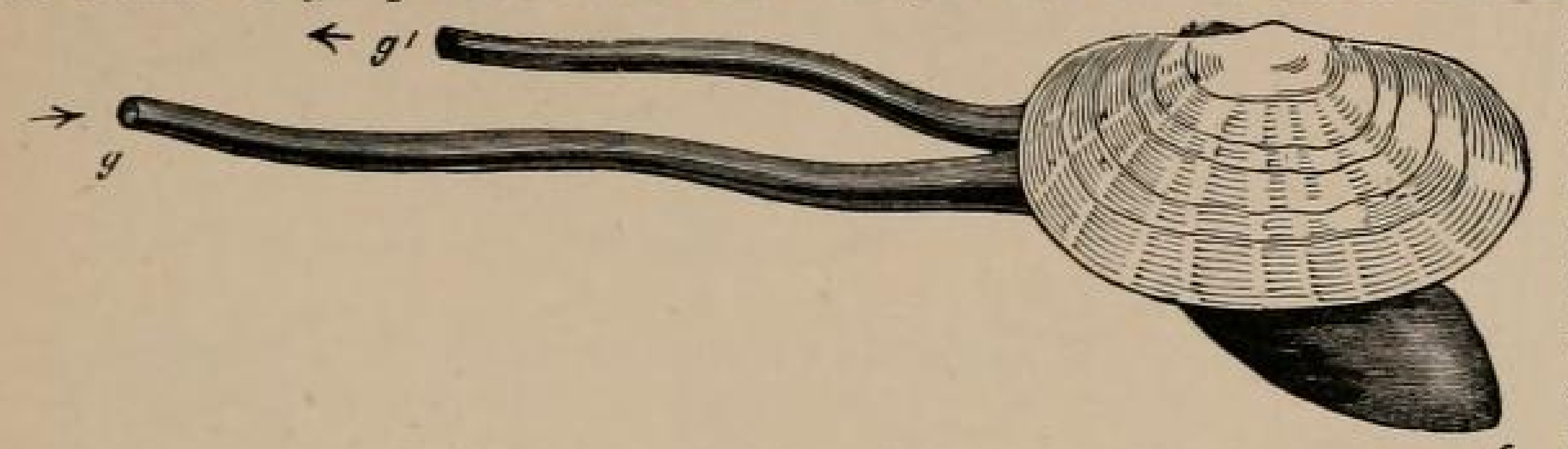

Fig 130.—*Psammobia florida*, right side, showing expanded foot *e*, and *g* incurrent and *g'* excurrent siphons (from Owen).

The labial tentacles of Anodon (*n*, *o* in fig. 124, (3), (5)) are highly vascular flat processes richly supplied with nerves. The left anterior tentacle (seen in the figure) is joined at its base in front of the mouth (*w*) to the right anterior tentacle, and similarly the left (*o*) and right posterior tentacles are joined behind the mouth. Those of Arca (*i*, *k* in fig. 132) show this relation to the mouth (*a*). These organs are characteristic of all Lamellibranchs; they do not vary except in size, being sometimes drawn out to streamer-like dimensions. Their appearance and position suggest that they are in some way related morphologically to the gill-plates, the anterior labial tentacle being a continuation of the outer gill-plate, and the posterior a continuation of the inner gill-plate. There is no embryological evidence to support this suggested connexion, and, as will appear immediately, the history of the gill-plates in various forms of Lamellibranchs does not directly favour it. Yet it is very probable that the labial tentacles and gill-plates are modifications of a double horseshoe-shaped area of ciliated filamentous processes which existed in ancestral Mollusca much as in Phoronis and the Polyzoa, and is to be compared with the continuous præ- and post-oral ciliated band of the Echinid larva Pluteus and of Tornaria (**49**).

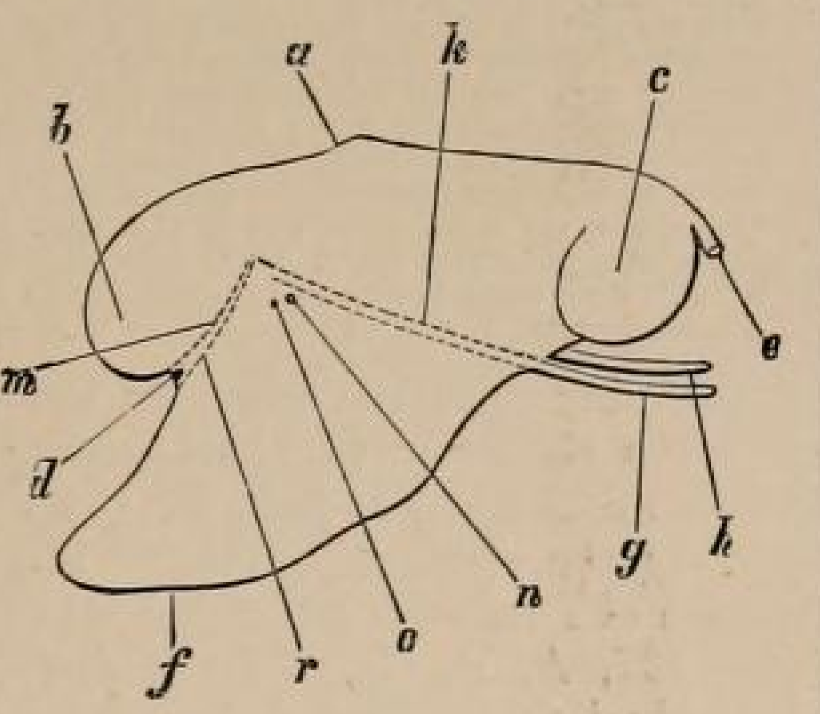

Fig. 131.—Diagram of a view from the left side of the animal of *Anodonta cygnæa*, from which the mantle-skirt, the labial tentacles, and the gill-filaments have been entirely removed so as to show the relations of the axis of the gill-plumes or ctenidia *g*, *h*. *a*, centro-dorsal area; *b*, anterior adductor muscle; *c*, posterior adductor muscle; *d*, mouth; *e*, anus; *f*, foot; *g*, free portion of the axis of left ctenidium; *h*, axis of right ctenidium; *k*, portion of the axis of the left ctenidium which is fused with the base of the foot, the two dotted lines indicating the origins of the two rows of gill-filaments; *m*, line of origin of the anterior labial tentacle; *n*, nephridial aperture; *o*, genital aperture; *r*, line of origin of the posterior labial tentacle. (Original.)

The gill-plates have a structure very different from that of the labial tentacles, and one which in Anodon is singularly complicated as compared with the condition presented by these organs in some other Lamellibranchs, and with what must have been their original condition in the ancestors of the whole series of living Lamellibranchia. The phenomenon of "concrescence" which we have already had to note as showing itself so importantly in regard to the free edges of the mantle-skirt and the formation of the siphons, is what, above all things, has complicated the structure of the Lamellibranch ctenidium. Our present knowledge of the interesting series of modifications through which the Lamellibranch gill-plates have developed to their most complicated form is due to R. Holman Peck (**50**) and to Mitsukuri (**51**). The Molluscan ctenidium is typically, as shown in fig. 2, a plume-like structure, consisting of a vascular axis, on each side of which is set a row of numerous lamelliform or filamentous processes. These processes are hollow, and receive the venous blood from, and return it again aerated into, the hollow axis, in which an afferent and an efferent blood-vessel may be differentiated. In the genus Nucula (fig. 134), one of the Arcaceæ, we have an example of a Lamellibranch retaining this plume-like form of gill. In other Arcaceæ (*e.g.*, Arca and Pectunculus) the lateral processes which are set on the axis of the ctenidium are not lamellæ, but are slightly-flattened, very long tubes or hollow filaments. These filaments are so fine and are set so closely together that they appear to form a continuous membrane until examined with a lens. The microscope shows that the neighbouring filaments are held together by patches of cilia, called "ciliated junctions," which interlock with one another just as two brushes may be made to do. In fig. 133, A a portion of four filaments of a ctenidium of the Sea-Mussel (Mytilus) is represented, having precisely the same structure as those of Arca. The filaments of the gill (ctenidium) of Mytilus and Arca thus form two closely set rows which depend from the axis of the gill like two parallel plates. Further, their structure is profoundly modified by the curious condition of the free ends of the depending filaments. These are actually reflected at a sharp angle—

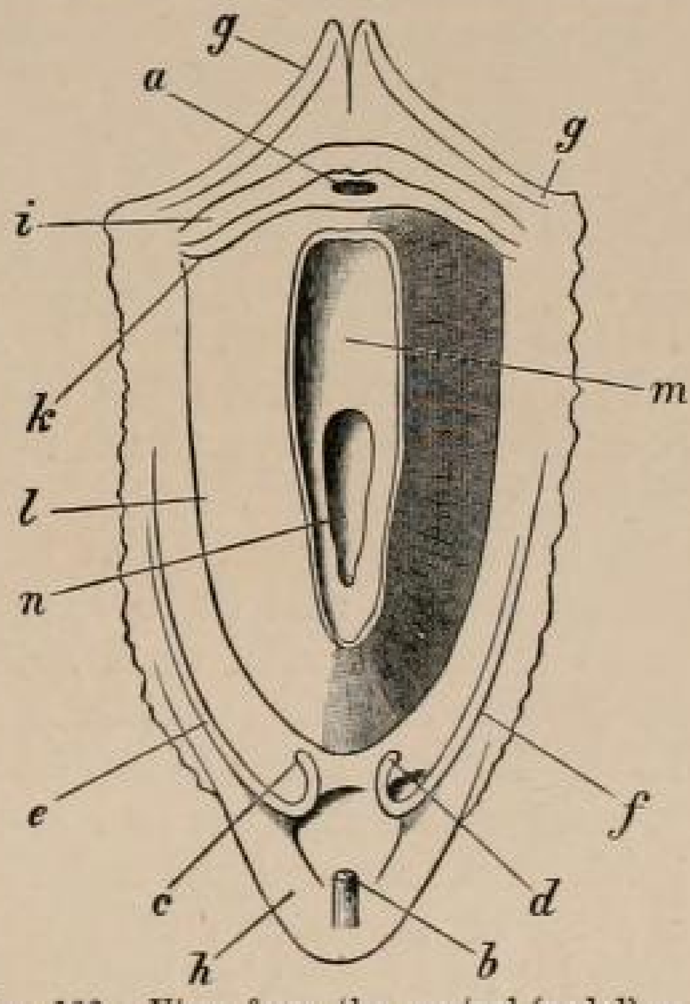

Fig. 132.—View from the ventral (pedal) aspect of the animal of *Arca Noæ*, the mantle-flap and gill-filaments having been cut away. *a*, mouth; *b*, anus; *c*, free spirally turned extremity of the gill-axis or ctenidial axis of the right side; *d*, do. of the left side; *e*, *f*, anterior portions of these axes fused by concrescence to the wall of the body; *g*, anterior adductor muscle; *h*, posterior adductor; *i*, anterior labial tentacle; *k*, posterior labial tentacle; *l*, base line of the foot; *m*, sole of the foot; *n*, callosity. (Original.)

doubled on themselves in fact—and thus form an additional row of filaments (see fig. 133, B). Consequently, each primitive filament has a descending and an ascending ramus, and instead of each row forming a simple plate, the plate is double, consisting of a descending and an ascending lamella. As the axis of the ctenidium lies by the side of the body, and is very frequently connate with the body, as so often happens in Gastropods also, we find it convenient to speak of the two plate-like structures formed on each ctenidial axis as the outer and the inner gill-plate; each of these is composed of two lamellæ, an outer (the reflected) and an adaxial in the case of the outer gill-plate, and an adaxial and an inner (the reflected) in the case of the inner gill-plate. This is the condition seen in Arca and Mytilus, the so-called plates dividing upon the slightest touch into their constituent filaments, which are but loosely conjoined by their "ciliated junctions." Complications follow upon this in other forms. Even in Mytilus and Arca a connexion is here and there formed between the ascending and descending rami of a filament by hollow extensible outgrowths called "interlamellar junctions" (*il.j* in B, fig. 133). Nevertheless the filament is a complete tube formed of chitonous substance and clothed externally by ciliated epithelium, internally by endothelium and lacunar tissue—a form of connective tissue—as shown in fig. 133, C. Now let us suppose, as happens in the genus Dreissena—a genus not far removed from Mytilus—that the ciliated inter-filamentar junctions (fig. 136) give place to solid permanent inter-filamentar junctions, so that the filaments are converted, as it were, into a trellis-work. Then let us suppose that the inter-lamellar junctions which we have already noted in Mytilus become very numerous, large, and irregular; by them the two trellis-works of filaments would be united so as to leave only a sponge-like set of spaces between them. Within the trabeculæ of the sponge-work blood circulates, and between the trabeculæ the water passes, having entered by the apertures left in the trellis-work formed by the united gill-filaments (fig. 138, A, B). The larger the intra-lamellar spongy growth becomes, the more do the original gill-filaments lose the character of blood-holding tubes and tend to become dense elastic rods for the simple purpose of supporting the spongy growth. This is seen both in the section of Dreissena gill (fig. 136) and in those of Anodon (fig. 137, A, B, C). In the drawing of Dreissena the individual filaments *f, f, f* are cut across in one lamella at the horizon of an inter-filamentar junction, in the other (lower in the figure) at a point where they are free. The chitonous substance *ch* is observed to be greatly thickened as compared with what it is in fig. 133, C, tending in fact to obliterate altogether the lumen of the filament. And in Anodon (fig. 137, C) this obliteration is effected. In Anodon, besides being thickened, the skeletal substance of the filament develops a specially dense rod-like body on each side of each filament. Although the structure of the ctenidium is thus highly complicated in Anodon, it is yet more so in some of the Siphonate genera of Lamellibranchs. The filaments take on a secondary grouping, the surface of the lamella being thrown into a series of half-cylindrical ridges, each consisting of ten or twenty filaments; a filament

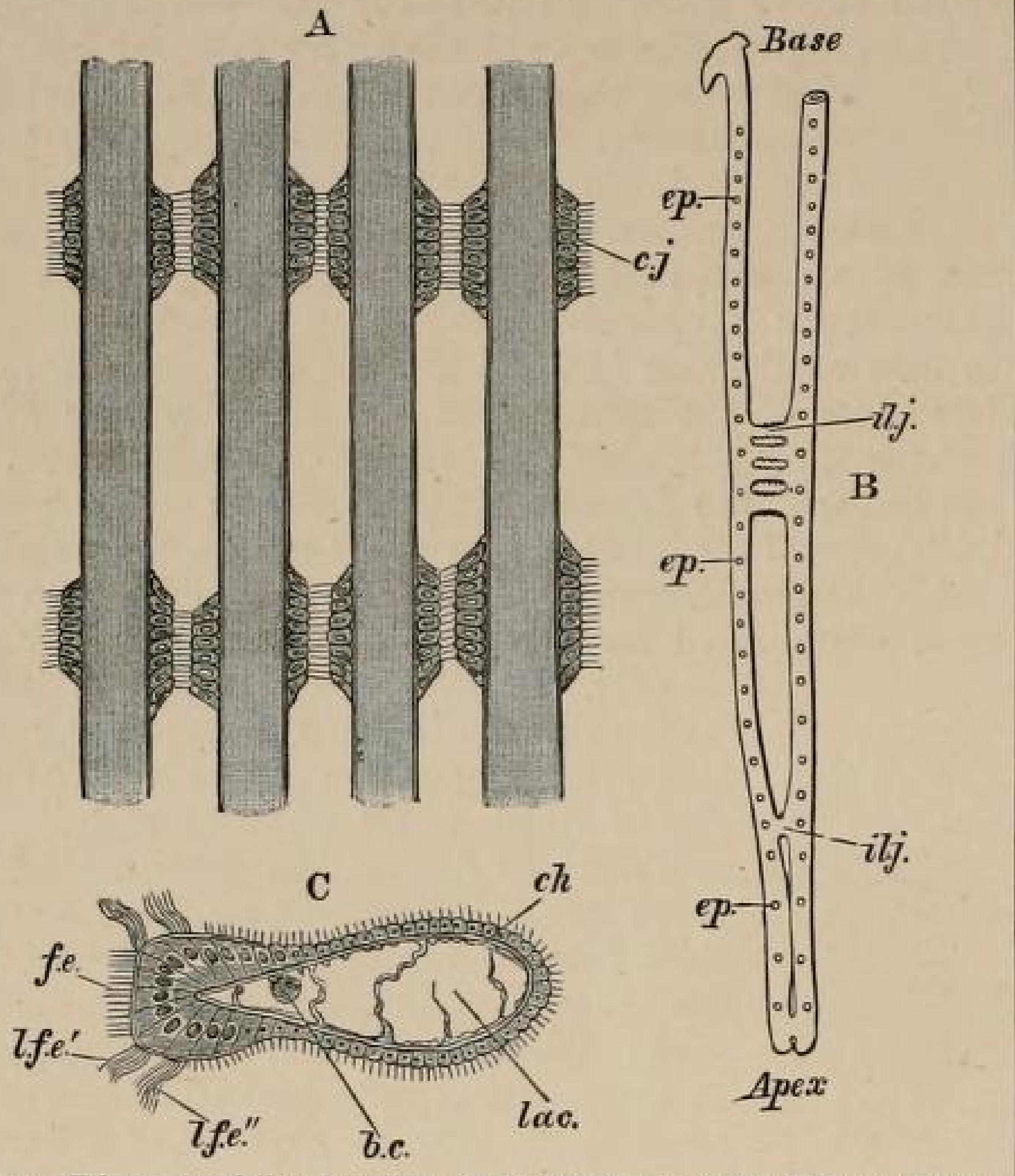

FIG. 133.—Filaments of the ctenidium of *Mytilus edulis* (after Holman Peck). A. Part of four filaments seen from the outer face in order to show the ciliated junctions *c.j.* B. Diagram of the posterior face of a single complete filament with descending ramus and ascending ramus ending in a hook-like process. *ep.*, *ep.*, the ciliated junctions; *il.j.*, inter-lamellar junction. C. Transverse section of a filament taken so as to cut neither a ciliated junction nor an inter-lamellar junction. *f.e.*, frontal epithelium; *l.f.e'.*, *l.f.e''.*, the two rows of latero-frontal epithelial cells with long cilia; *ch*, chitonous tubular lining of the filament; *lac.*, blood lacuna traversed by a few processes of connective tissue cells; *b.c.*, blood-corpuscle.

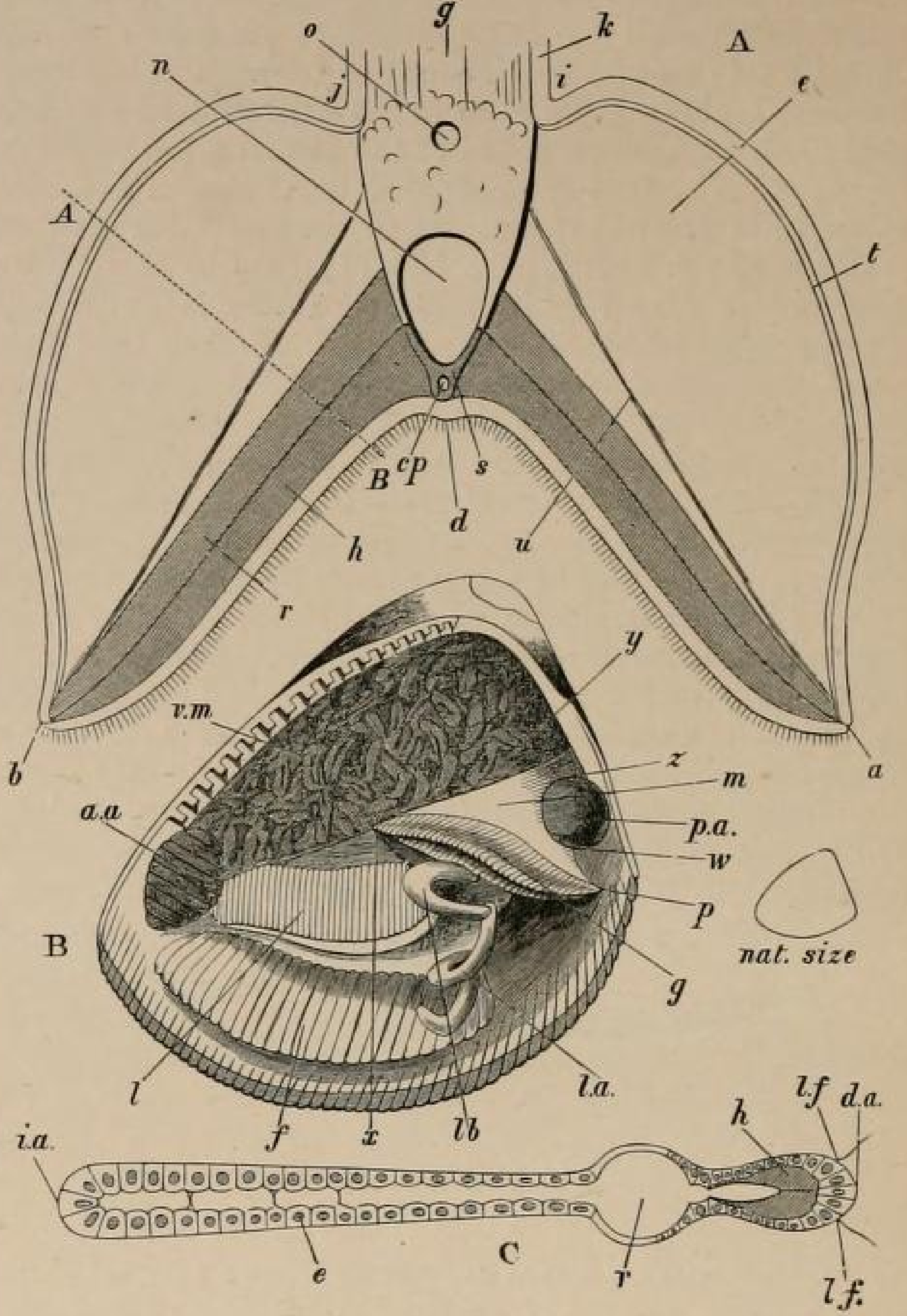

FIG. 134.—Structure of the ctenidia of Nucula (after Mitsukuri); see also fig. 2. A. Section across the axis of a ctenidium with a pair of plates—flattened and shortened filaments—attached. *i*, *j*, *k*, *g* are placed on or near the membrane which attaches the axis of the ctenidium to the side of the body; *a*, *b*, free extremities of the plates (filaments); *d*, mid-line of the inferior border; *e*, surface of the plate; *t*, its upper border; *h*, chitonous lining of the plate; *r*, dilated blood-space; *u*, fibrous tract; *o*, upper blood-vessel of the axis; *n*, lower blood-vessel of the axis; *s*, chitonous framework of the axis; *cp*, canal in the same; *A*, *B*, line along which the cross-section C of the plate is taken. B. Animal of a male *Nucula proxima*, Say, as seen when the left valve of the shell and the left half of the mantle-skirt are removed. *a.a.*, anterior adductor muscle; *p.a.*, posterior adductor muscle; *v.m*, visceral mass; *f*, foot; *g*, gill; *l*, labial tentacle; *l.a.*, filamentous appendage of the labial tentacle; *lb*, hood-like appendage of the labial tentacle; *m*, membrane suspending the gill and attached to the body along the line *x*, *y*, *z*, *w*; *p*, posterior end of the gill (ctenidium). C. Section across one of the gill-plates (*A*, *B*, in A) comparable with fig. 133, C. *i.a.*, outer border; *d.a.*, axial border; *l.f.*, latero-frontal epithelium; *e*, epithelium of general surface; *r*, dilated blood-space; *h*, chitonous lining (compare A).

of much greater strength and thickness than the others may be placed between each pair of groups. In Anodon, as in many other Lamellibranchs, the ova and hatched embryos are carried for a time in the ctenidia or gill apparatus, and in this particular case the space between the two lamellæ of the outer gill-plate is that which serves to receive the ova (fig. 137, A). The young are nourished by a substance formed by the cells which cover the spongy inter-lamellar outgrowths.

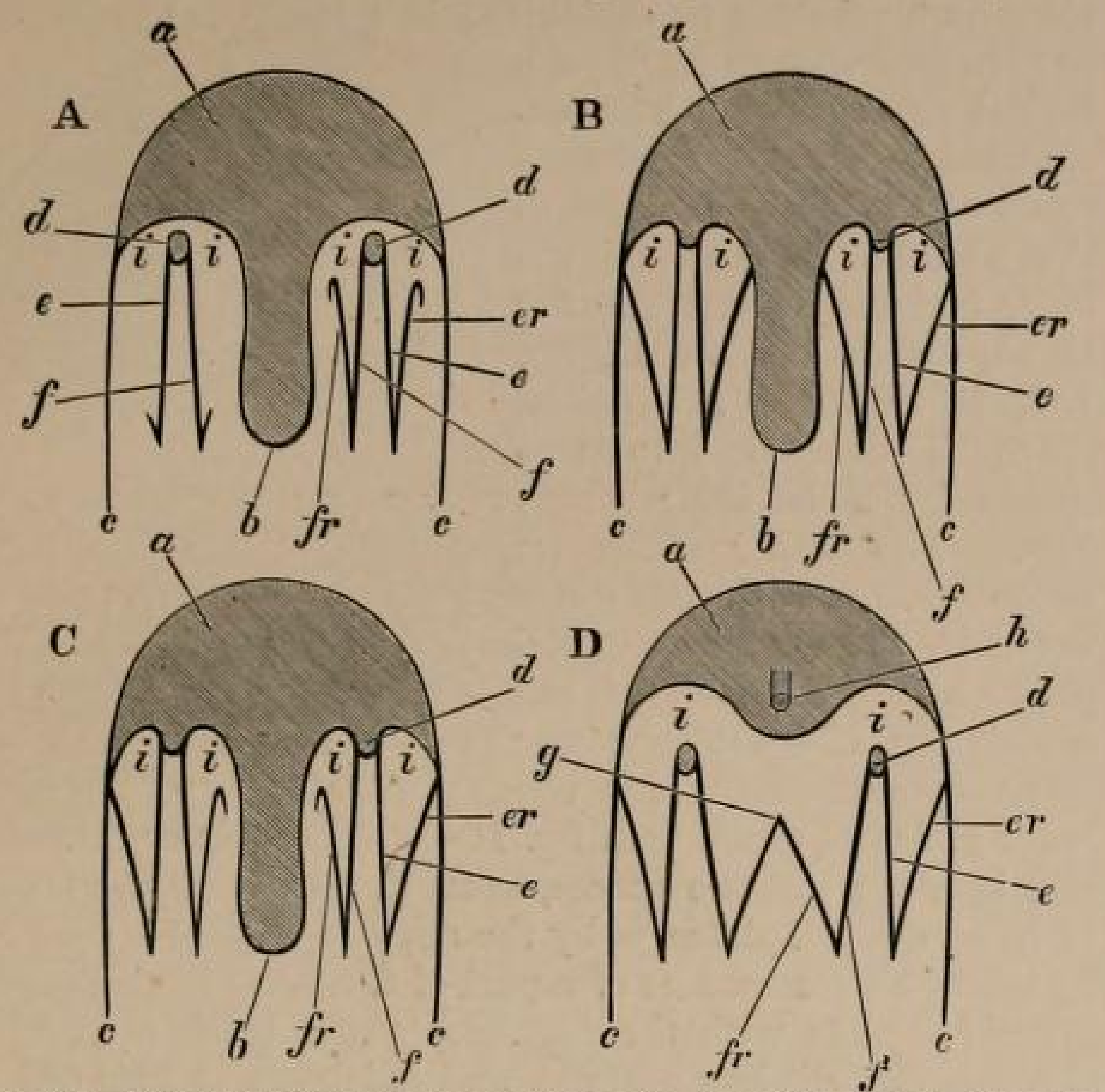

FIG. 135.—Diagrams of transverse sections of a Lamellibranch to show the adhesion, by concrescence, of the gill-lamellæ to the mantle-flaps, to the foot, and to one another. A shows two conditions with free gill-axis; B, condition at foremost region in Anodon; C, hind region of foot in Anodon; D, region altogether posterior to the foot in Anodon. *a*, visceral mass; *b*, foot; *c*, mantle flap; *d*, axis of gill or ctenidium; *e*, adaxial lamella of outer gill-plate; *er*, reflected lamella of outer gill-plate; *f*, adaxial lamella of inner gill-plate; *fr*, reflected lamella of inner gill-plate; *g*, line of concrescence of the reflected lamellæ of the two inner gill-plates; *h*, rectum; *i*, supra-branchial space of the sub-pallial chamber. (Original.)

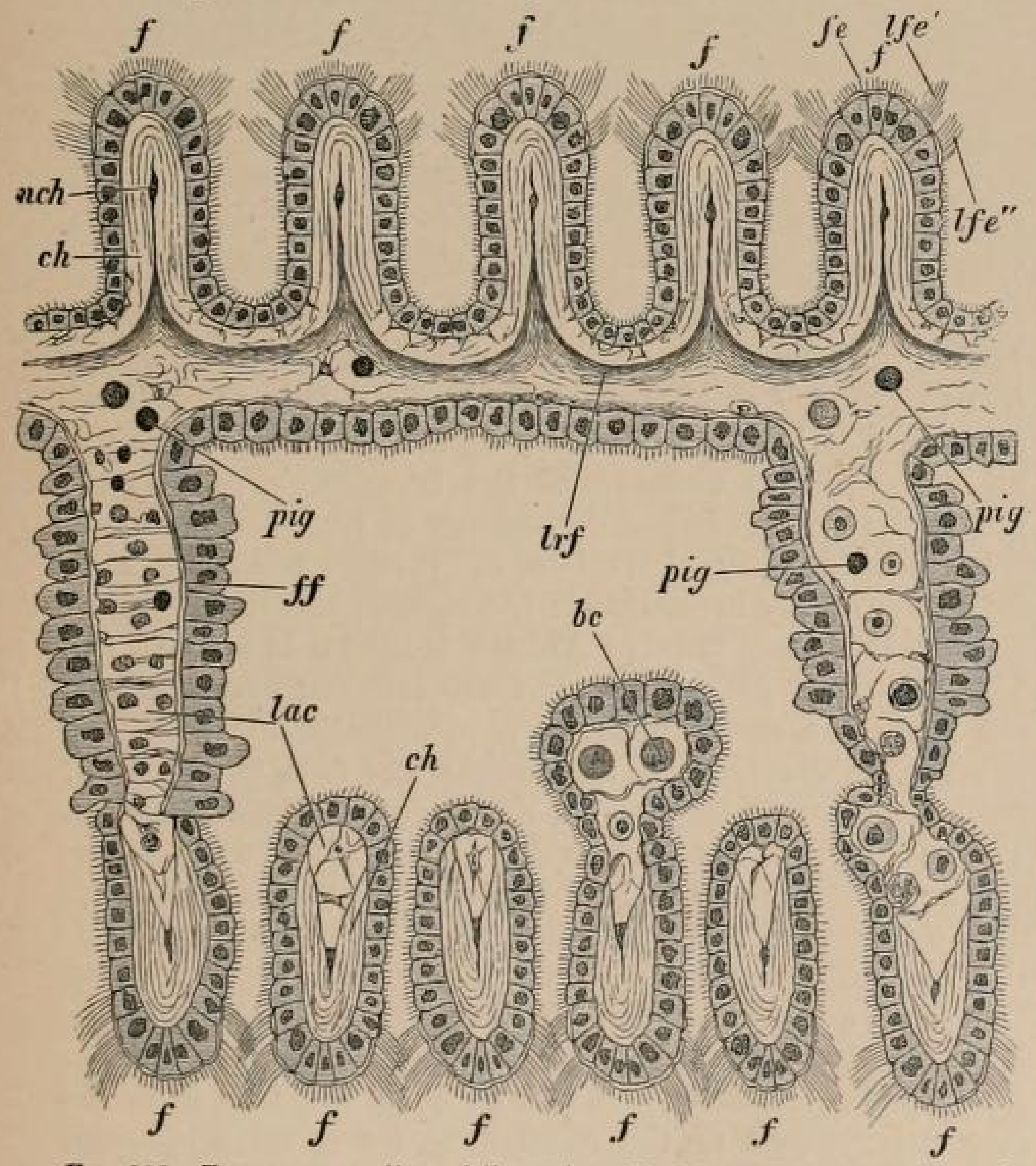

FIG. 136.—Transverse section of the outer gill-plate of *Dreissena polymorpha* (after Holman Peck). *f*, constituent gill-filaments; *ff*, fibrous sub-epidermic tissue; *ch*, chitonous substance of the filaments; *nch*, cells related to the chitonous substance; *lac*, lacunar tissue; *pig*, pigment-cells; *bc*, blood-corpuscles; *fe*, frontal epithelium; *lfe'*, *lfe''*, two rows of latero-frontal epithelial cells with long cilia; *lrf*, fibrous, possibly muscular, substance of the inter-filamenter junctions.

There are certain other points in the modification of the typical ctenidium which must be noted in order to understand the ctenidium of Anodon. The axis of each ctenidium, right and left, starts from a point well forward near the labial tentacles, but it is at first only a ridge, and does not project as a free cylindrical axis until the back part of the foot is reached. This is difficult to see at all in Anodon, but if the mantle-skirt be entirely cleared away, and if the dependent lamellæ which spring from the ctenidial axis be carefully cropped away so as to leave the axis itself intact, we obtain the form shown in fig. 131, where *g* and *h* are respectively the left and the right ctenidial axes projecting freely beyond the body. In Arca this can be seen with far less trouble, for the filaments are more easily removed than are the consolidated lamellæ formed by the filaments of Anodon, and in Arca the free axes of the ctenidia are large and firm in texture (fig. 132, *c*, *d*).

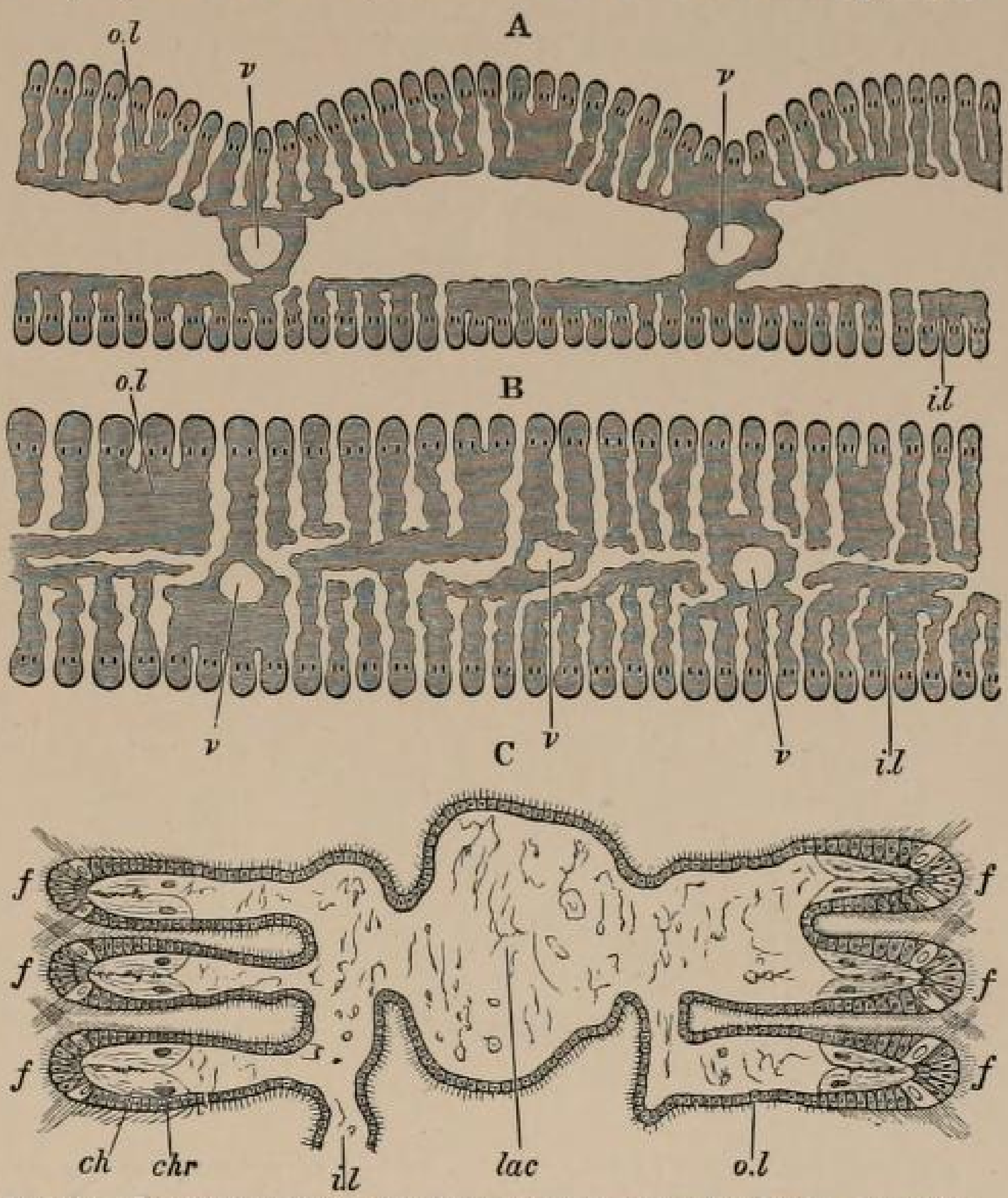

FIG. 137.—Transverse sections of gill-plates of Anodon (after Peck). A. Outer gill-plate. B. Inner gill-plate. C. A portion of B more highly magnified. *o.l*, outer lamella; *i.l*, inner lamella; *v*, blood-vessel; *f*, constituent filaments; *lac*, lacunar tissue; *ch*, chitonous substance of the filament; *chr*, chitonous rod embedded in the softer substance *ch*.

If we were to make a vertical section across the long axis of a Lamellibranch which had the axis of its ctenidium free from its origin onwards, we should find such relations as are shown in the diagram fig. 135, A. The gill axis *d* is seen lying in the sub-pallial chamber between the foot *b* and the mantle *c*. From it depend the gill-filaments or lamellæ—formed by united filaments—drawn as black lines *f*. On the left side these lamellæ are represented as having only a small reflected growth, on the right side the reflected ramus or lamella is complete (*fr* and *er*). The actual condition in Anodon at the region where the gills commence anteriorly is shown in fig. 135, B. The axis of the ctenidium is seen to be adherent to, or fused by concrescence with, the body-wall, and moreover on each side the outer lamella of the outer gill-plate is fused to the mantle, whilst the inner lamella of the inner gill-plate is fused to the foot. If we pass a little backwards and take another section nearer the hinder margin of the foot, we get the arrangement shown diagrammatically in fig. 135, C, and more correctly in fig. 142. In this region the inner lamellæ of the inner gill-plates are no longer affixed to the foot.

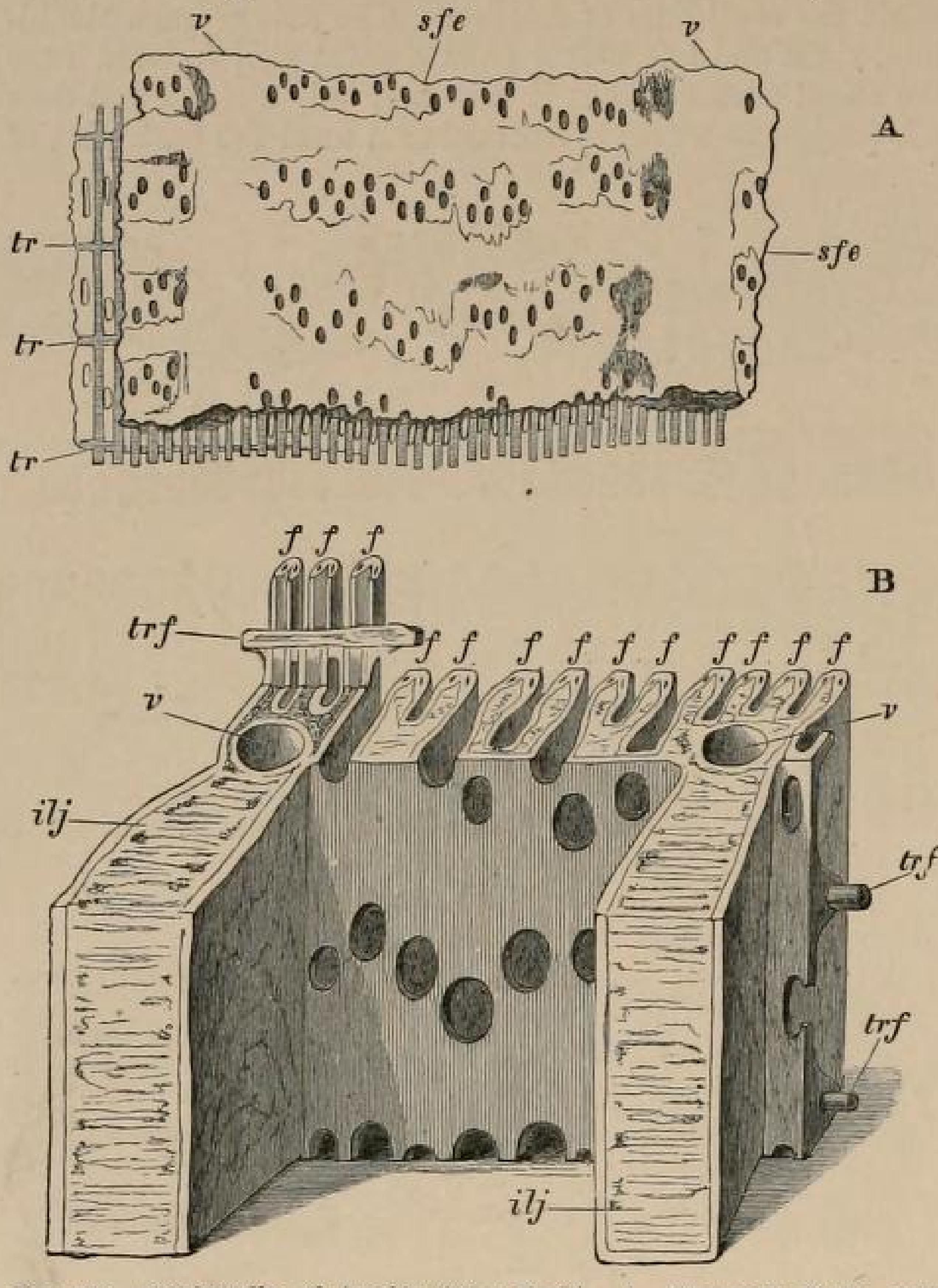

FIG. 138.—Gill-lamellæ of Anodon (after Peck). A. Fragment of the outer lamella of an inner gill-plate torn from the connected inner lamella, the sub-filamentar tissue also partly cut away round the edges so as to expose the filaments, their transverse junctions *tr*, and the "windows" left in the lattice-work; *sfe*, internal surface of the lamella; *v*, vessel. B. Diagram of a block cut from the outer lamella of the outer gill-plate and seen from the inter-lamellar surface (after Peck). *f*, constituent filaments; *trf*, fibrous tissue of the transverse inter-filamentar junctions; *v*, blood-vessel; *ilj*, inter-lamellar junction. The series of oval holes on the back of the lamella are the water-pores which open between the filaments in irregular rows separated horizontally by the transverse inter-filamentar junctions.

Passing still further back behind the foot, we find in Anodon the condition shown in the section D, fig. 135. The axes *i* are now free; the outer lamellæ of the outer gill-plates (*er*) still adhere by concrescence to the mantle-skirt, whilst the inner lamellæ of the inner gill-plates meet one another and fuse by concrescence at *g*. In the lateral view of the animal with reflected mantle-skirt and gill-plates, the line of concrescence of the inner lamellæ of the inner gill-plates is readily seen; it is marked *aa* in fig. 124, (5).

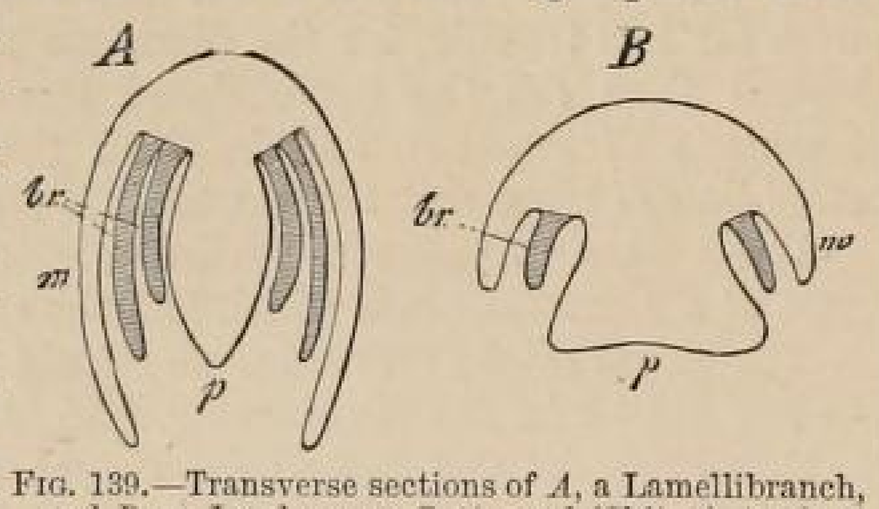

FIG. 139.—Transverse sections of *A*, a Lamellibranch, and *B*, an Isopleurous Gastropod (Chiton), to show the relations of *p*, the foot; *br*, the branchiæ; and *m*, the mantle. (From Gegenbaur.)

In the same figure the free part of the inner lamella of the inner gill-plate resting on the foot is marked *z*, whilst the attached part—the most anterior—has been snipped with scissors so as to show the genital and nephridial apertures *x* and *y*. The concrescence, then, of the free edge of the reflected lamellæ of the gill-plates of Anodon is very extensive. It is important, because such a concrescence is by no means universal, and does not occur, for example, in Mytilus or in Arca; further, because when its occurrence is once appreciated, the reduction of the gill-plates of Anodon to the plume-type of the simplest ctenidium presents no difficulty; and, lastly, it has importance in reference to its physiological significance.

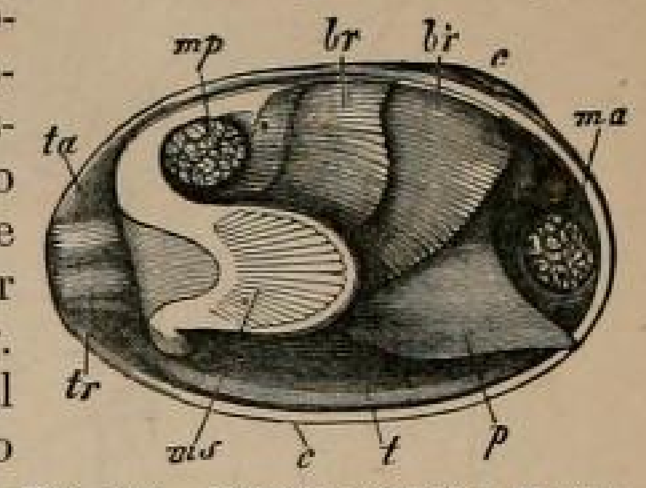

FIG. 140.—Lateral view of a Mactra, the right valve of the shell and right mantle-flap removed, and the siphons retracted. *br*, *br'*, outer and inner gill-plates; *t*, labial tentacle; *ta*, *tr*, upper and lower siphons; *ms*, siphonal muscle of the mantle-flap; *ma*, anterior adductor muscle; *mp*, posterior adductor muscle; *p*, foot; *c*, umbo. (From Gegenbaur.)

The mechanical result of the concrescence of the outer lamellæ to the mantle-flap, and of the inner lamellæ to one another as shown in section D, fig. 135, is that the sub-pallial space is divided into two spaces by a horizontal septum. The upper space (*i*) communicates with the outer world by the excurrent or superior siphonal notch of the mantle (fig. 124, *d*); the lower space communicates by the lower siphonal notch (*e* in fig. 124). The only communication between the two spaces, excepting through the trellis-work of the gill-plates, is by the slit (*z* in fig. 124, (5)) left by the non-concrescence of a part of the inner lamella of the inner gill-plate with the foot. A probe (*g*) is introduced through this slit-like passage, and it is seen to pass out by the excurrent siphonal notch. It is through this passage, or indirectly through the pores of the gill-plates, that the water introduced into the lower sub-pallial space must pass on its way to the excurrent siphonal notch. Such a subdivision of the pallial chamber, and direction of the currents set up within it do not exist in a number of Lamellibranchs which have the gill-lamellæ comparatively free (Mytilus, Arca, Trigonia, &c.), and it is in these forms that there is least modification by concrescence of the primary filamentous elements of the lamellæ. Probably the gill-structure of Lamellibranchs will ultimately furnish some classificatory characters of value when they have been thoroughly investigated throughout the class.

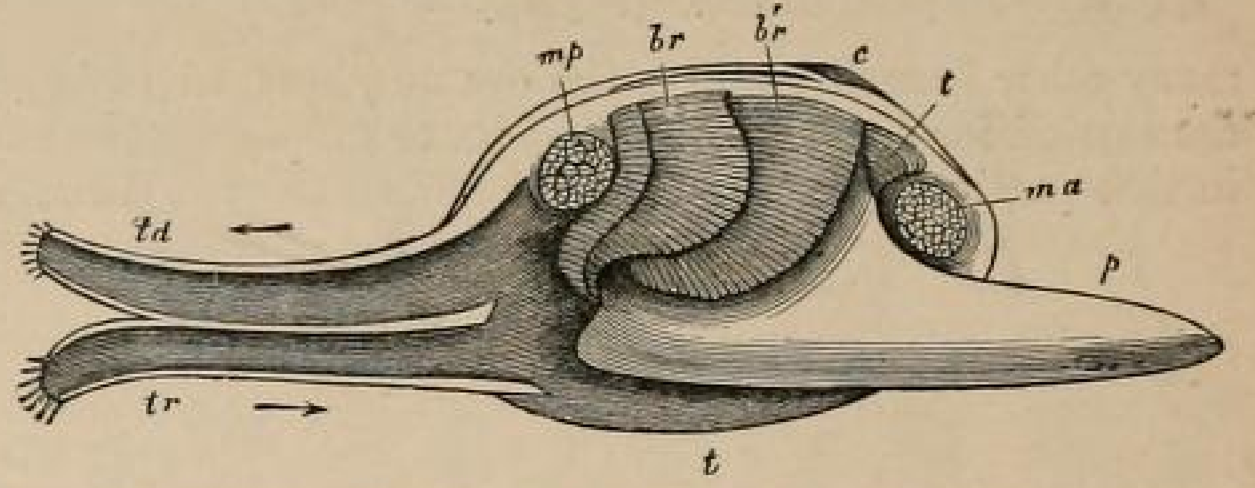

FIG. 141.—The same animal as fig. 140, with its foot and siphons expanded. Letters as in fig. 140. (From Gegenbaur.)

The alimentary canal of Anodon is shown in fig. 124, (4). The mouth is placed between the anterior adductor and the foot; the anus opens on a median papilla overlying the posterior adductor, and discharges into the superior pallial chamber along which the excurrent stream passes. The coil of the intestine in Anodon is similar to that of other Lamellibranchs, but the crystalline style and its diverticulum are not present here. The rectum traverses the pericardium, and has the ventricle of the heart wrapped, as it were, around it. This is not an unusual arrangement in Lamellibranchs, and a similar disposition occurs in some Gastropoda (Haliotis). A pair of ducts (*ai*) lead from the first enlargement of the alimentary tract called stomach into a pair of large digestive glands, the so-called liver, the branches of which are closely packed in this region (*af*). The food of the Anodon, as of other Lamellibranchs, consists of microscopic animal and vegetable organisms, which are brought to the mouth by the stream which sets into the sub-pallial chamber at the lower siphonal notch (*e* in fig. 124). Probably a straining of water from solid particles is effected by the lattice-work of the ctenidia or gill-plates.

The heart of Anodon consists of a median ventricle embracing the rectum (fig. 143, A), and giving off an anterior and a posterior artery, and of two auricles which open into the ventricle by orifices protected by valves.

The blood is colourless, and has colourless amœboid corpuscles floating in it. In two Lamellibranchs, *Solen* (*Ceratisolen*) *legumen* and *Arca Noæ*, the blood is crimson, owing to the presence of corpuscles impregnated with hæmoglobin (Lankester, **31**). In Anodon the blood is driven by the ventricle through the arteries into vessel-like spaces, which soon become irregular lacunæ surrounding the viscera, but in parts—*e.g.*, the labial tentacles and walls of the gut—very fine vessels with endothelial cell-lining are found. The blood makes its way by large veins to a venous sinus which lies in the middle line below the heart, having the paired renal organs (nephridia) placed between it and that organ. Hence it passes through the vessels of the glandular walls of the nephridia right and left into the gill-lamellæ, whence it returns through many openings into the widely-stretched auricles. A great deal more precision has been given to accounts of the structure of arteries, veins, and capillaries in Anodon than the facts warrant. The course of the blood-stream can only be somewhat vaguely inferred except in its largest outlines. Distinct arterial and venous channels cannot be distinguished in the gill-lamellæ, in spite of what Langer (**52**) has written on the subject, though it is highly probable that there is some kind of circulation in the gills. In the filaments of the gill of Mytilus the tubular cavity is divided by a more or less complete fibrous septum into two channels, presumably for an ascending and a descending blood-current. The ventricle and auricles of Anodon lie in a pericardium which is clothed with a pavement endothelium (*d*, fig. 143). Veins are said by Keber and others to open anteriorly into it, but this appears to be an error. It does not contain blood or communicate directly with the blood-system; this isolation of the pericardium we have noted already in Gastropods and Cephalopods. A good case for the examination of the question as to whether blood enters the pericardium of Lamellibranchs, or escapes from the foot, or by the renal organs when the animal suddenly contracts, is furnished by the *Solen legumen*, which has red blood-corpuscles. According to observations made by Penrose (**53**) on an uninjured *Solen legumen*, no red corpuscles are to be seen in the pericardial space, although the heart is filled with them, and no such corpuscles are ever discharged by the animal when it is irritated.

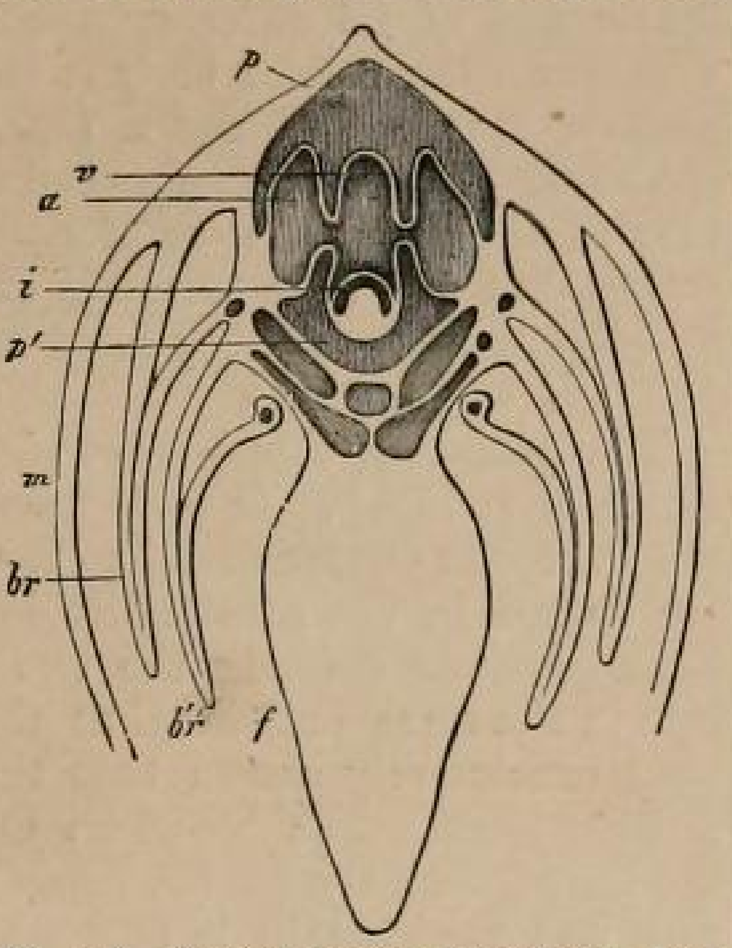

FIG. 142.—Vertical section through an Anodonta, about the mid-region of the foot. *m*, mantle-flap; *br*, outer, *b′r′*, inner gill-plate—each composed of two lamellæ; *f*, foot; *v*, ventricle of the heart; *a*, auricle; *p*, *p′*, pericardial cavity; *i*, intestine.

The pair of nephridia of Anodon, called in Lamellibranchs the organ of Bojanus, lie below the membranous floor of the pericardium, and open into it by two well-marked apertures (*e* and *f* in fig. 143). Each nephridium, after being bent upon itself as shown in fig. 143, C, D, opens to the exterior by a pore placed at the point marked *x* in fig. 124, (5), (6). It is no doubt possible, as in the Gastropoda and Cephalopoda, for water to enter from the exterior by the nephridia into the pericardium, but that it ever does so is as yet not proved. What is certain from the set of the ciliary currents is that liquid generally passes out of the pericardium by the nephridia. One half of each nephridium is of a dark-green colour and glandular (*h* in fig. 143). This opens into the reflected portion which overlies it as shown in the diagram fig. 143, D, *i*; the latter has non-glandular walls, and opens by the pore *k* to the exterior. The nephridia may be more ramified in other Lamellibranchs than they are in Anodon. In some they are difficult to discover. That of the common oyster has recently (1882) been detected by Hoek (**54**). Each nephridium in the oyster is a pyriform sac, which communicates by a narrow canal with the urino-genital groove placed to the front of the great adductor muscle; by a second narrow canal it communicates with the pericardium. From all parts of the pyriform sac narrow stalk-like tubes are given off, ending in abundant widely-spread branching glandular cæca, which form the essential renal secreting apparatus. The genital duct opens by a pore into the urino-genital groove of the oyster (the same arrangement being repeated on each side of the body) close to but distinct from the aperture of the nephridial canal. Hence, except for the formation of a urino-genital groove, the apertures are placed as they are in Anodon. Previously to Hoek's discovery a brown-coloured investment of the auricles of the heart of the oyster had been supposed to represent the nephridia in a rudimentary state. This investment, which occurs also in Mytilus but not in Anodon, may possibly consist of secreting cells, and may be comparable to the pericardial accessory glandular growths of Cephalopoda.

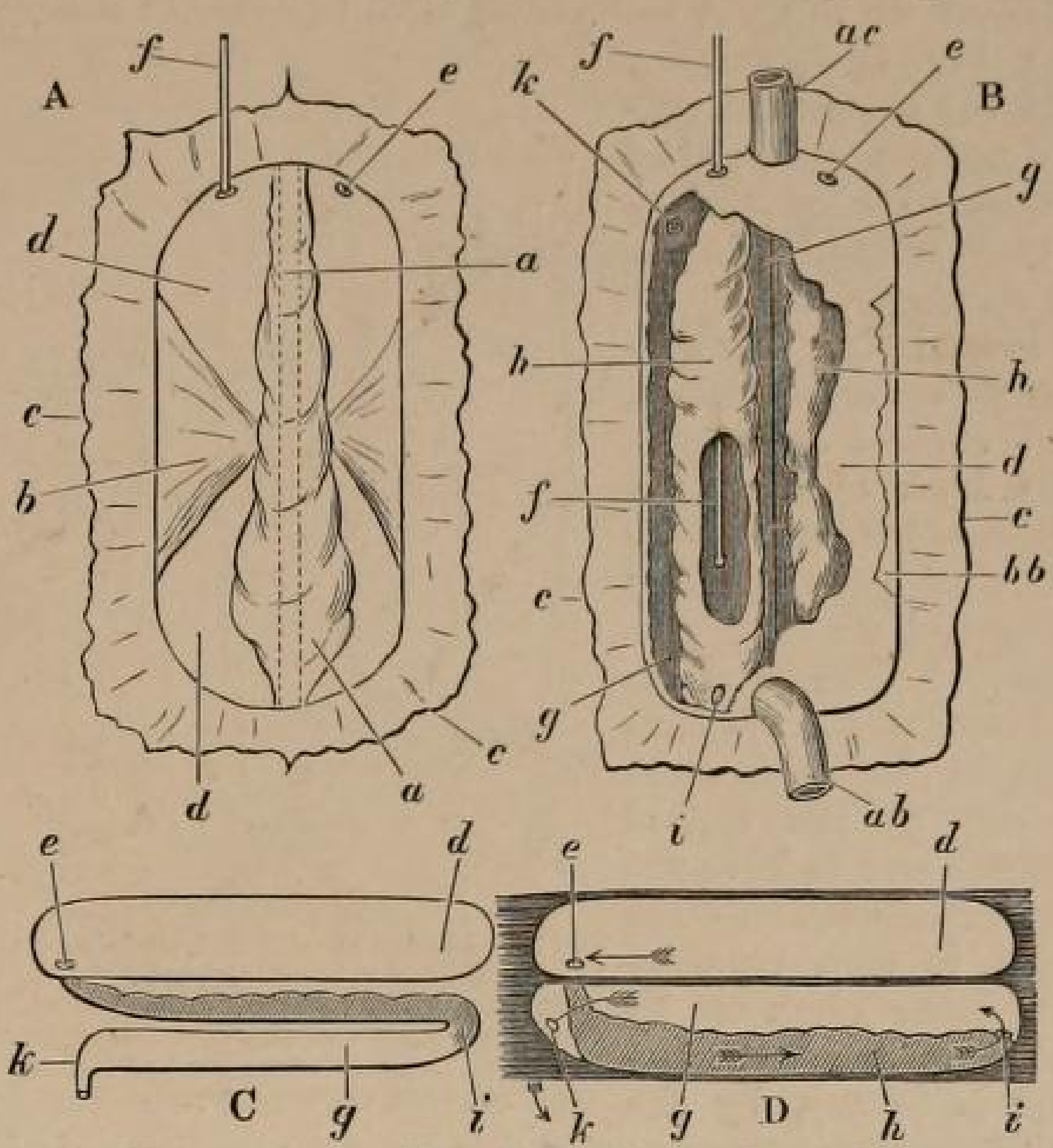

FIG. 143.—Diagrams showing the relations of pericardium and nephridia in a Lamellibranch such as Anodon. A. Pericardium opened dorsally so as to expose the heart and the floor of the pericardial chamber *d*. B. Heart removed and floor of the pericardium cut away on the left side so as to open the non-glandular sac of the nephridium, exposing the glandular sac *b*, which is also cut into so as to show the probe *f*. C. Ideal pericardium and nephridium viewed laterally. D. Lateral view showing the actual relation of the glandular and non-glandular sacs of the nephridium. The arrows indicate the course of fluid from the pericardium outwards. *a*, ventricle of the heart; *b*, auricle; *bb*, cut remnant of the auricle; *c*, dorsal wall of the pericardium cut and reflected; *e*, reno-pericardial orifice; *f*, probe introduced into the left reno-pericardial orifice; *g*, non-glandular sac of the left nephridium; *h*, glandular sac of the left nephridium; *i*, pore leading from the glandular into the non-glandular sac of the left nephridium; *k*, pore leading from the non-glandular sac to the exterior; *ac*, anterior, *ab*, posterior, cut remnants of the intestine and ventricle.

Nervous System and Sense-organs.—In Anodon there are three well-developed pairs of nerve-ganglia (fig. 144, B and fig. 124, (6)). An anterior pair, lying one on each side of the mouth (fig. 144, B, *a*) and connected in front of it by a commissure, are the representatives of the cerebral, pleural, and visceral ganglia of the typical Mollusc, which are not here differentiated as they are in Gastropods (compare, however, fig. 67). A pair placed close together in the foot (fig. 144, B, *b*, and fig. 124, (6), *ax*) are the typical pedal ganglia; they are joined to the cerebro-pleuro-visceral ganglia by connectives.

Posteriorly beneath the posterior adductors, and covered only by a thin layer of elongated epidermal cells, are the olfactory ganglia, their epidermal clothing constituting the pair of osphradia, which are thus seen in Lamellibranchs to occupy their typical position and to have the typical innervation,—the nerve to each osphradium being given off by the visceral ganglion—that is to say, by the undifferentiated cerebro-pleuro-visceral ganglion of its proper side. This identification of the posterior ganglion-pair of Lamellibranchs is due to Spengel (**11**). Other anatomists have considered this ganglion-pair as corresponding to either the pleural or the visceral of Gastropoda, or to both, and very usually it is termed "the parieto-splanchnic" (Huxley).

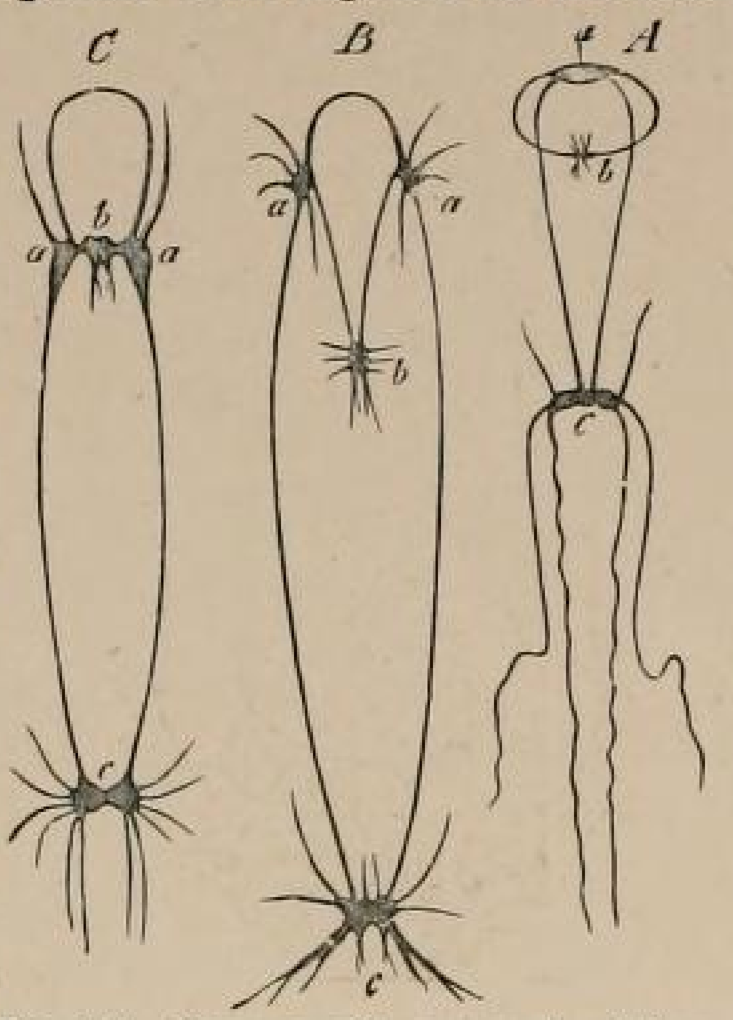

FIG. 144.—Nerve-ganglia and cords of three Lamellibranchs (from Gegenbaur): *A*, of Teredo; *B*, of Anodonta; *C*, of Pecten. *a*, cerebral ganglion-pair (=cerebro-pleuro-visceral); *b*, pedal ganglion-pair; *c*, olfactory (osphradial) ganglion-pair.

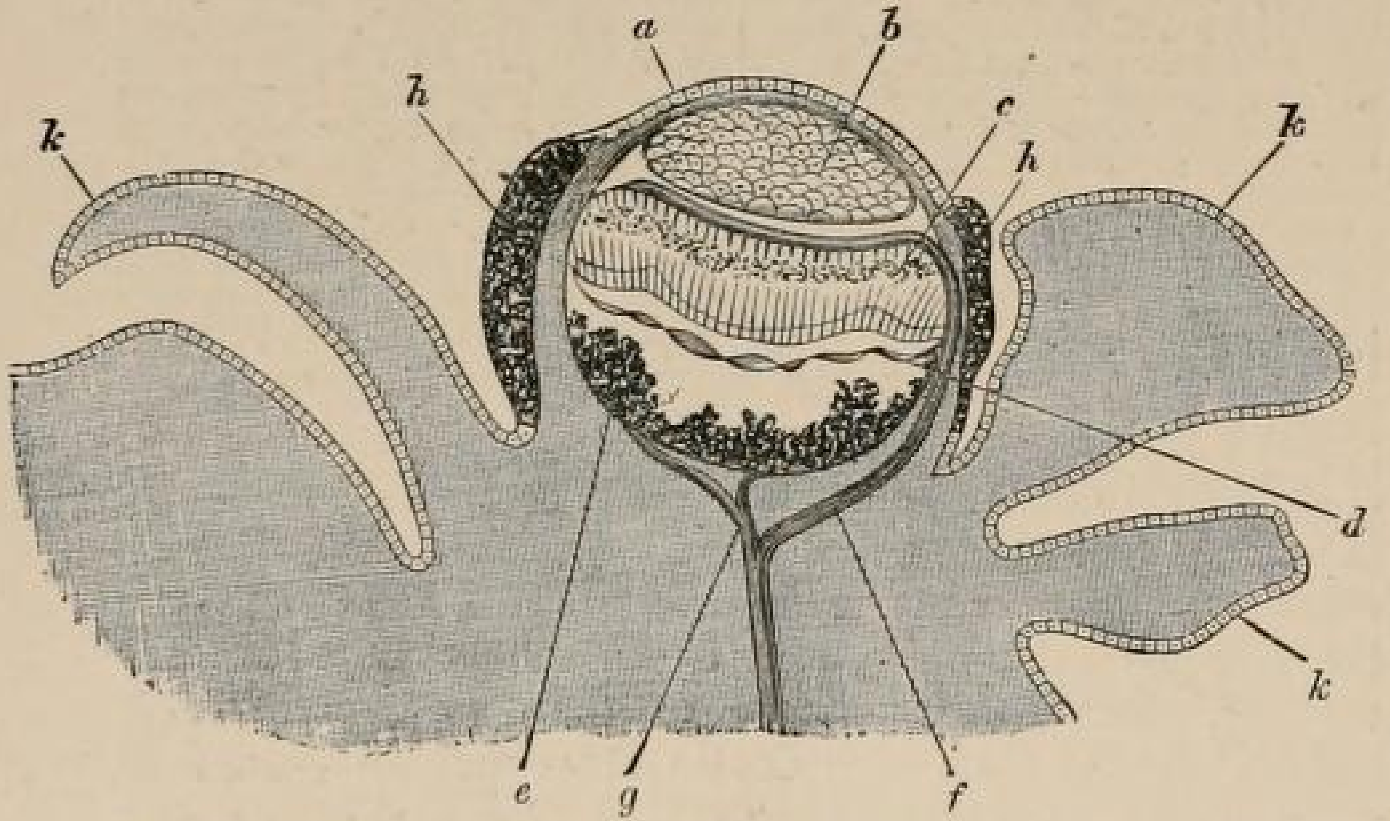

FIG. 145.—Pallial eye of Spondylus (from Hickson). *a*, præ-corneal epithelium; *b*, cellular lens; *c*, retinal body; *d*, tapetum; *e*, pigment; *f*, retinal nerve; *g*, complementary nerve; *h*, epithelial cells filled with pigment; *k*, tentacle

The sense-organs of Anodon other than the osphradia consist of a pair of otocysts attached to the pedal ganglia (fig. 124, (6), *ay*). The otocysts of Cyclas are peculiarly favourable for study on account of the transparency of the small foot in which they lie, and may be taken as typical of those of Lamellibranchs generally. The structure of one is exhibited in fig. 146. A single otolith is present as in the veliger embryos of Opisthobranchia. In adult Gastropoda there are frequently a large number of rod-like otoliths instead of one.

Anodon has no eyes of any sort, and the tentacles on the mantle edge are limited to its posterior border. This deficiency is very usual in the class; at the same time, many Lamellibranchs have tentacles on the edge of the mantle supplied by a pair of large well-developed nerves, which are given off from the cerebro-pleuro-visceral ganglion-pair, and very frequently some of these tentacles have undergone a special metamorphosis converting them into highly-organized eyes. Such eyes on the mantle-edge are found in Pecten, Spondylus, Lima, Ostrea (?), Pinna, Pectunculus, Modiola, Mytilus (?), Cardium, Tellina, Mactra, Venus, Solen, Pholas, and Galeomma. They are totally distinct from the cephalic eyes of typical Mollusca, and have a different structure and historical development. They have not originated as pits but as tentacles. They agree with the dorsal eyes of Onchidium (Pulmonata) in the curious fact that the optic nerve penetrates the capsule of the eye and passes in front of the retinal body (fig. 145), so that its fibres join the anterior faces of the nerve-end cells as in Vertebrates, instead of their posterior faces as in the cephalic eyes of Mollusca and Arthropoda; moreover, the lens is not a cuticular product but a cellular structure, which, again, is a feature of agreement with the Vertebrate eye. It must, however, be distinctly borne in mind that there is a fundamental difference between the eye of Vertebrates and of all other groups in the fact that in the Vertebrata the retinal body is itself a part of the central nervous system, and not a separate modification of the epidermis—myelonic as opposed to epidermic. The structure of the reputed eyes of several of the above-named genera has not been carefully examined. In Pecten and Spondylus, however, they have been fully studied (see fig. 145, and explanation).

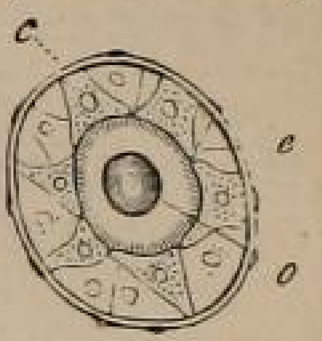

FIG. 146.—Otocyst of Cyclas (from Gegenbaur). *c*, capsule; *e*, ciliated cells lining the same; *o*, otolith.

The gonads of Anodon are placed in distinct male and female individuals. In some Lamellibranchs—for instance, the European Oyster and the *Pisidium pusillum*—the sexes are united in the same individual; but here, as in most hermaphrodite animals, the two sexual elements are not ripe in the same individual at the same moment. It has been conclusively shown that the *Ostrea edulis* does not fertilize itself. The American Oyster (*O. virginiana*) and the Portuguese Oyster (*O. angulata*) have the sexes separate, and fertilization is effected in the open water after the discharge of the ova and the spermatozoa from the females and males respectively. In the *Ostrea edulis* fertilization of the eggs is effected at the moment of their escape from the uro-genital groove, or even before, by means of spermatozoa drawn into the sub-pallial chamber by the incurrent ciliary stream, and the embryos pass through the early stages of development whilst entangled between the gill-lamellæ of the female parent (fig. 6). In Anodon the eggs pass into the space between the two lamellæ of the outer gill-plate, and are there fertilized, and advance whilst still in this position to the glochidium phase of development (fig. 147). They may be found here in thousands in the summer and autumn months. The gonads themselves are extremely simple arborescent glands which open to the exterior by two simple ducts, one right and one

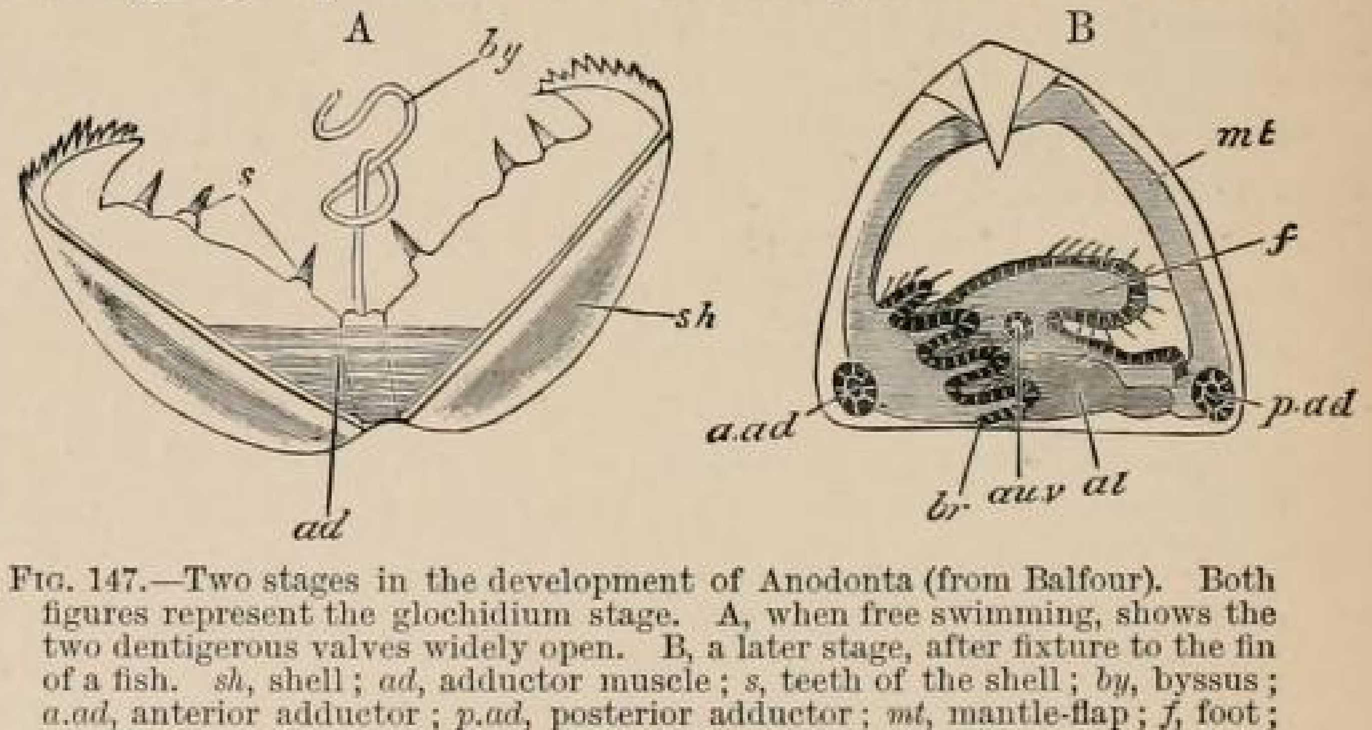

FIG. 147.—Two stages in the development of Anodonta (from Balfour). Both figures represent the glochidium stage. A, when free swimming, shows the two dentigerous valves widely open. B, a later stage, after fixture to the fin of a fish. *sh*, shell; *ad*, adductor muscle; *s*, teeth of the shell; *by*, byssus; *a.ad*, anterior adductor; *p.ad*, posterior adductor; *mt*, mantle-flap; *f*, foot; *br*, branchial filaments; *au.v*, otocyst; *al*, alimentary canal.

left, continuous with the wall of the tubular branches of the gland (fig. 124, (5), (6), *y*). In no Lamellibranch is there a divergence from this structure, excepting that in some (Ostrea) the contiguous nephridial and the genital aperture are sunk in a urino-genital groove, which in other cases (Spondylus?) may partially close up so as to constitute a single pore for the nephridial and genital ducts. No accessory genital glands are present.

The development of Anodon is remarkable for the curious larval form known as Glochidium (fig. 147). The Glochidium quits the gill-pouch of its parent and swims by alternate opening and shutting of the valves of its shell, as do adult Pecten and Lima, trailing at the same time a long byssus thread. By this it is brought into contact with the fin of a fish, such as Perch, Stickleback, or others, and effects a hold thereon by means of the toothed edge of its shells. Here it becomes encysted, and is nourished by the exudations of the fish. A distinct development of its internal organs has been traced by the late Professor Balfour, but no one has followed it to the moment at which it drops from the fish's fin and assumes the form of shell characteristic of the parent. Other Lamellibranchs exhibit either a trochosphere larva which becomes a Veliger, differing only from the Gastropod's and Pteropod's Veliger in having bilateral shell-calcifications instead of a single central one; or, like Anodon, they may develop within the gill-plates of the mother, though without presenting such a specialized larva as the Glochidium. An example of the former is seen in the development of the European Oyster, to the figure of which and its explanation the reader is specially referred (fig. 6). An example of the latter is seen in a common little fresh-water bivalve, the *Pisidium pusillum*, which has been studied by Lankester (**12**). The successive stages of the development of this Lamellibranch are illustrated in the woodcuts figs. 148 to 153 inclusive. These should be compared with the figures of Gastropod development (figs. 3, 4, 5, 7, and 72***). Fig. 148 shows the cleavage of the egg-cell into four (A), and at a later stage the tucking in of some of the cells to form an invaginated series (B).

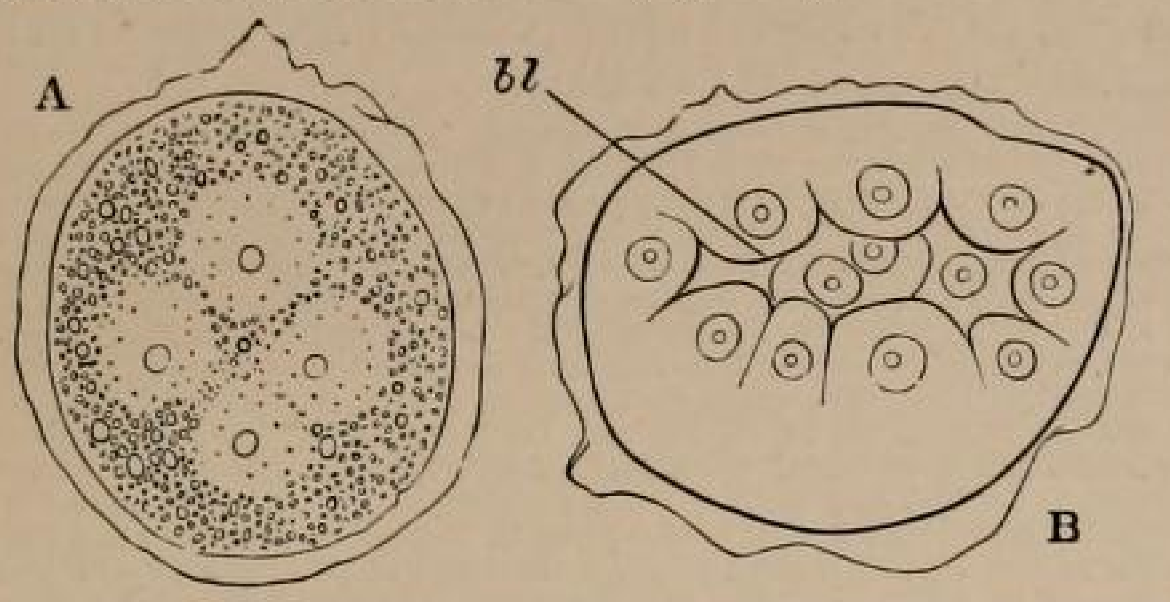

Fig. 148.—Embryos of *Pisidium pusillum* (after Lankester). A. Only four embryonic cells are present, still enclosed in the egg envelope. B. The cells have multiplied and commenced to invaginate, forming a blastopore or orifice of invagination, *bl*.

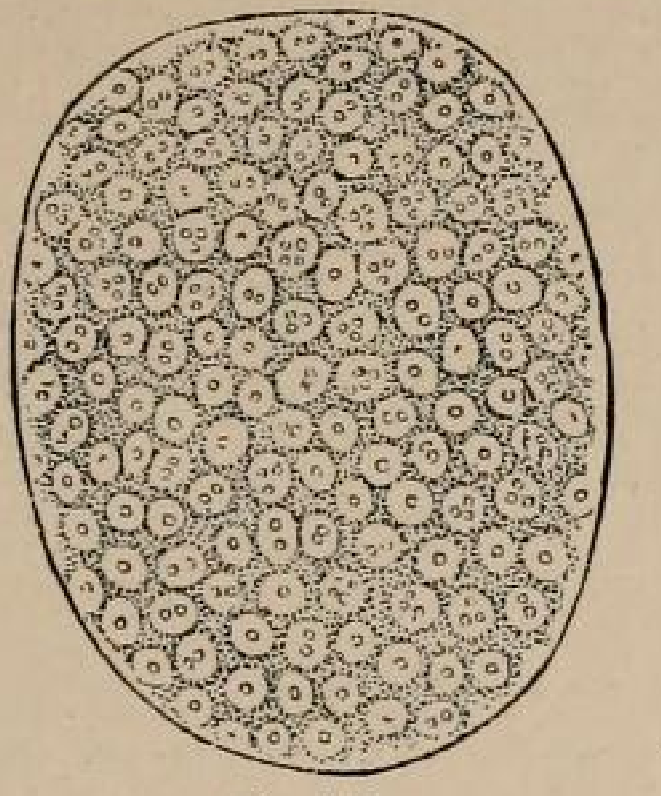

Fig. 149.

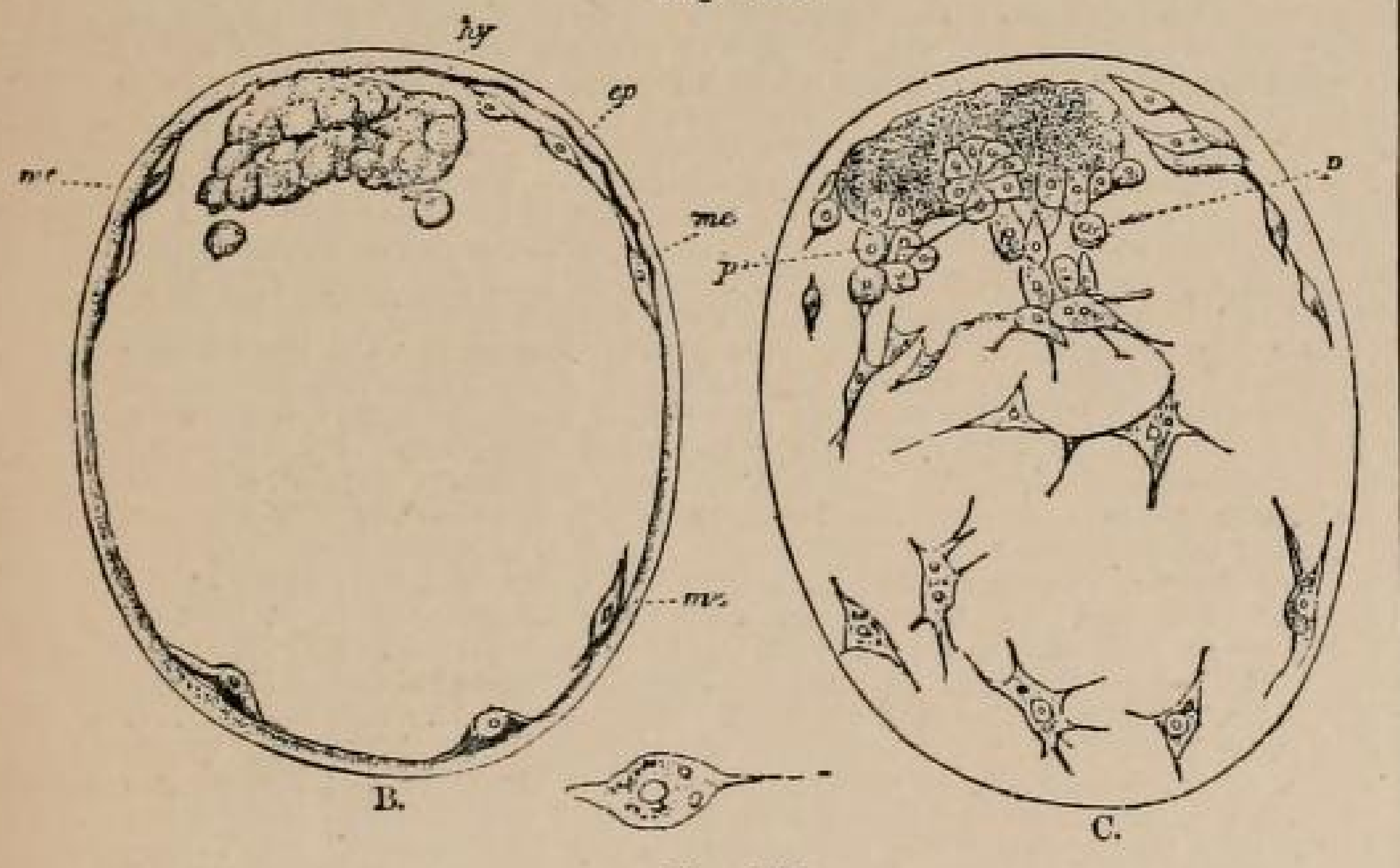

Fig. 150.

Fig. 149.—Embryo of *Pisidium pusillum* in the diblastula stage, surface view (after Lankester). The embryo has increased in size by accumulation of liquid between the outer and the invaginated cells. The blastopore has closed.

Fig. 150.—B. Same embryo as fig. 149, in optical median section, showing the invaginated cells *hy* which form the arch-enteron, and the mesoblastic cells *me* which are budded off from the surface of the mass *hy*, and apply themselves to the inner surface of the deric or epiblastic cell-layer *ep*. C. The same embryo focused so as to show the mesoblastic cells which immediately underlie the outer cell-layer.

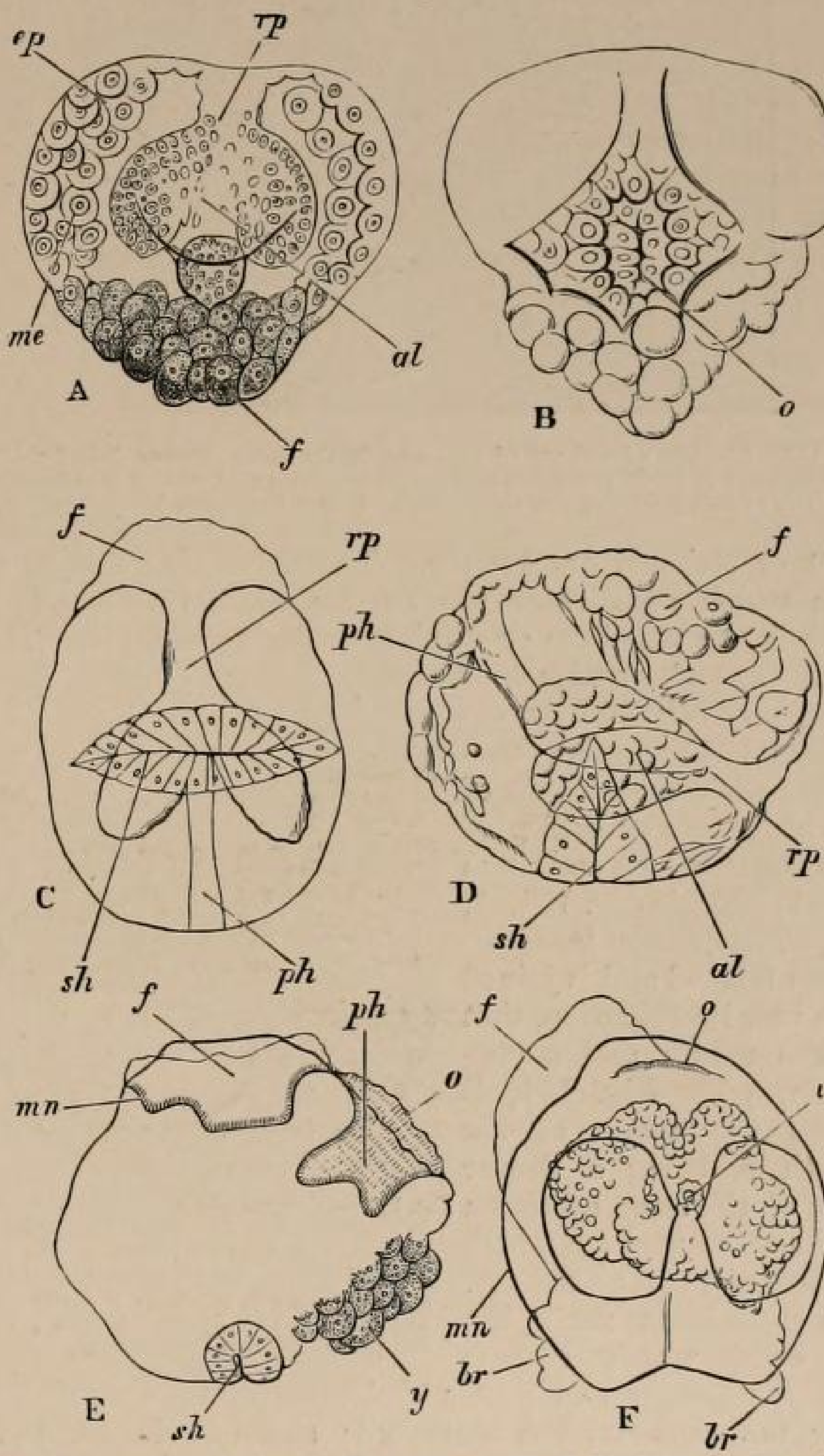

Fig. 151.—Further stages in the development of *Pisidium pusillum* (after Lankester). A. Optical section of an embryo in which the foot has begun to develop. B. The same embryo focused to its surface plane to show the mouth *o*. C. Later embryo, showing the shell-gland *sh*. D. Lateral view of the same embryo. E. Later stage, with rudiments of the mantle-flap, lateral view. F. Still later stage, with shell-valves and branchial filaments. *ep*, epiblast; *me*, mesoblast; *al*, met-enteron; *rp*, rectal peduncle or pedicle of invagination connecting the met-enteron with the cicatrix of the blastopore; *o*, mouth; *ph*, pharynx; *sh*, shell-gland; *mn*, mantle-flap; *br*, branchial filaments; *y*, granular cells of doubtful significance; *v*, vesicular structure of unknown significance.

The embryonic cells continue to divide, and form an oval vesicle containing liquid (fig. 149); within this, at one pole, is seen the mass of invaginated cells (fig. 150, *hy*). These invaginated cells are the arch-enteron; they proliferate and give off branching cells, which apply themselves (fig. 150, C) to the inner face of the vesicle, thus forming the mesoblast or cœlomic outgrowths. The outer single layer of cells which constitutes the surface of the vesicle (fig. 147) is the ectoderm or epiblast or deric cell-layer. The little mass of hypoblast or enteric cell-mass now enlarges, but remains connected with the cicatrix of the blastopore or orifice of invagination by a stalk, the rectal peduncle (fig. 151, A, *rp*). The enteron itself becomes bilobed and is joined by a new invagination, that of the mouth and stomodæum, *ph*. Fig. 151, B shows the origin of the mouth *o*, being a deeper view of the same specimen in the same position which is drawn in fig. 151, A. The mesoblast multiplies its cells, which become partly muscular and partly skeleto-trophic. Centro-dorsally now appears the embryonic shell-gland (fig. 151, C, *sh*). The pharynx or stomodæum is still small, the foot not yet prominent. A later stage is seen in fig. 152, where the pharynx is widely open and the foot prominent. No ciliated velum or præ-oral (cephalic) lobe ever develops. The shell-gland disappears, the mantle-skirt is raised as a ridge (fig. 151, E, *mn*), the paired shell-valves are secreted, the anus opens by a proctodæal ingrowth into the rectal peduncle, and the rudiments of the gills (*br*) and of the nephridia (B) appear (figs. 151, F, and 153, dorsal and lateral views of same stage), and thus the chief organs and general form of the adult are acquired. Later changes, not drawn here, consist in the growth of the shell-valves over the whole area of the mantle-flaps, and in the multiplication of the gill-filaments and their consolidation to form gill-plates. It is important to note that the gill-filaments are formed one by one *posteriorly*. The labial tentacles are formed late. In the allied genus Cyclas, a byssus gland is formed in the foot and subsequently disappears, but no such gland occurs in Pisidium. The nerve-ganglia and the otocysts probably form from thickenings of the epiblast, but detailed observation on this and other points of histogenesis in the Lamellibranchia is still wanting.

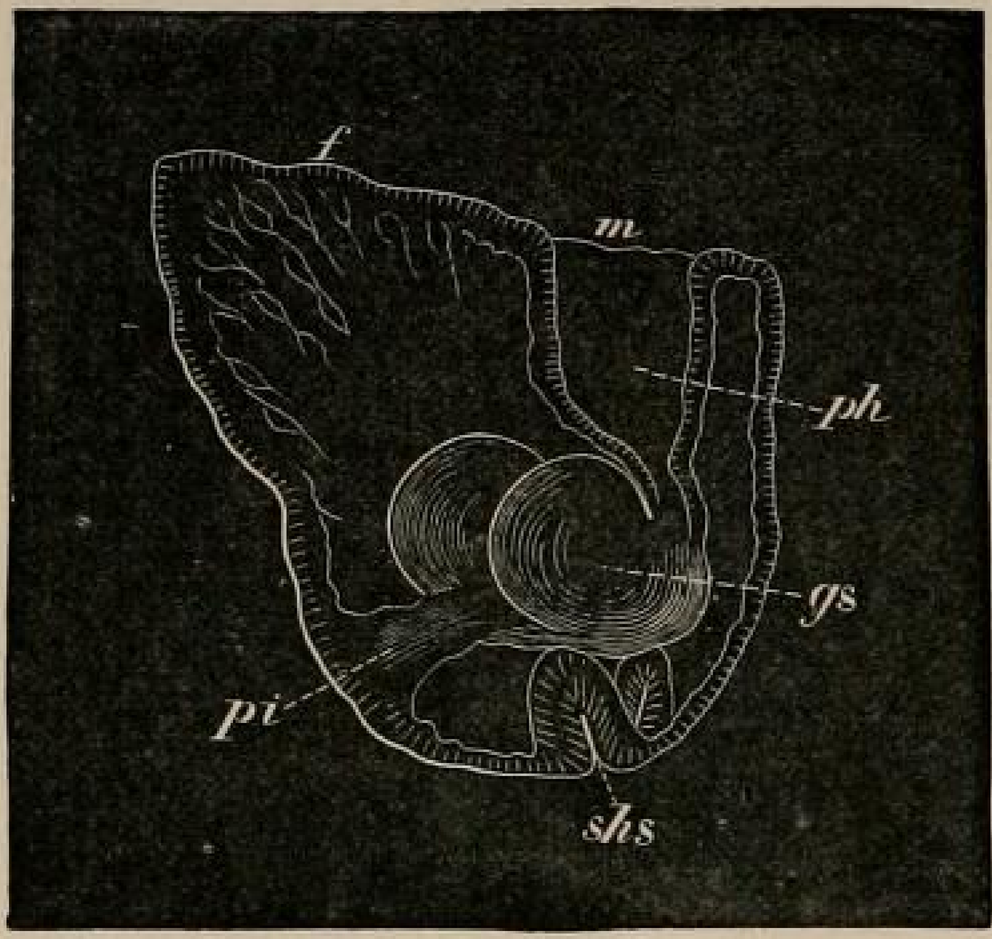

FIG. 152.—Diagram of embryo of Pisidium in the same stage as E in fig. 151. *m*, mouth; *f*, foot; *ph*, pharynx; *gs*, met-enteron; *pi*, rectal peduncle or pedicle of invagination; *shs*, shell-gland. (From Lankester.)

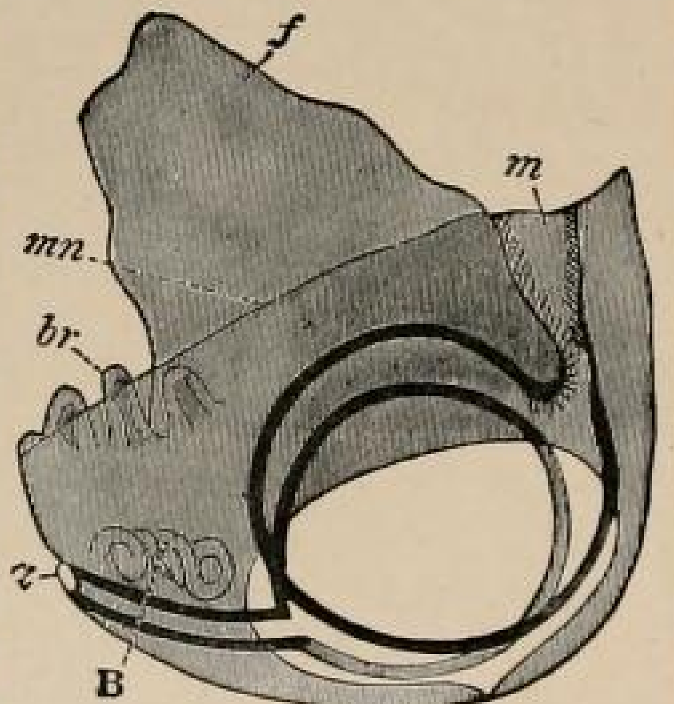

FIG. 153.—Diagram of embryo of Pisidium, in same stage as F in fig. 151 (after Lankester). *m*, mouth; *x*, anus; *f*, foot; *br*, branchial filaments; *mn*, margin of the mantle-skirt; *B*, organ of Bojanus (nephridium). The unshaded area gives the position of the shell-valve.

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